UNIVERSITE PAUL CEZANNE AIX-MARSEILLE III

N°……

Dynamiques des forêts denses humides et des savanes en réponse aux incendies en Nouvelle-Calédonie

THESE
pour obtenir le grade de

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Résumé

La Nouvelle-Calédonie qui présente une biodiversité à la fois exceptionnelle et très menacée, fait partie des points chauds de biodiversités définis à l'échelle globale comme zones prioritaires pour la conservation. Les incendies, d'origines anthropiques et constituant l'une des principales menaces pesant sur les écosystèmes naturels néo-calédoniens, conduisent à un recul des forêts denses humides (forêts par la suite) principalement au profit des savanes sur substrats volcano-sedimentaires. Au cours de cette thèse, les processus écologiques mis en jeu dans les dynamiques des forêts et des savanes, liés aux variations du régime d'incendie, ont été étudiés à différentes échelles spatiales et temporelles. L'analyse de la distribution spatio-temporelle des forêts et des savanes à l'échelle du paysage a mis en évidence différents facteurs dirigeant la dynamique paysagères et identifié des zones de recolonisation forestière. Différents modèles de succession secondaire et cortèges d'espèces pionnières ont été identifiés à partir de l'analyse de ces zones de recolonisation. La mesure de traits fonctionnels et l'utilisation de modèles semi-physiques de dommages causés par les incendies ont révélé une faible tolérance aux incendies de ces espèces. Enfin, une analyse multivariée de la structure, de la composition floristique et des conditions micro-climatiques des zones clés de transitions entre la savane et la forêt a permis de mieux comprendre les processus d'expansion et de contraction forestière. Ces travaux de thèse ouvrent un nouveau champ de recherche en Nouvelle-Calédonie avec d'importantes implications en terme de restauration des écosystèmes forestiers et de gestion durable.

Sciences de l'environnement

Mots-clés : Succession secondaire, restauration, analyses de communautés, assemblages floristique, effet de bords, traits fonctionnels de résistance au feu, dispersion, structures de populations.

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Rainforest and savanna dynamics in response to fires in New Caledonia

Abstract

New Caledonia, which presents both an exceptional and highly endangered biodiversity, is one of the worldwide biodiversity hotspots for conservation priority. Human-induced fires, which are one of the main threats to natural ecosystems in New Caledonia, lead to the expansion of savannas on volcano-sedimentary substrates at the expense of rainforests. In this thesis, the ecological processes, which are involved in the dynamics of rainforests and savannas and related to changes in fire regime, have been studied at different spatial and temporal scales. The analysis of the spatio-temporal distribution of rainforests and savannas across the landscape allowed us to both point-out the different drivers of their dynamics and to identify areas of rainforest recolonization. Different secondary succession patterns and pioneer species assemblages were identified from the analysis of these areas of recolonization. The analysis of measured functional traits and the use of semi-physical models of fire-caused damages highlighted the low tolerance of these pioneer species to fire. Finally, a multivariate analysis of the structure, the floristic composition and the micro-climatic conditions of transitional zones between savanna and rainforest, has allowed us to better understand the processes of rainforest's expansion and contraction. This thesis opens a new field of research in New Caledonia with important implications in rainforest's restoration and sustainable management.

Environmental sciences

Keywords: Secondary succession, restoration, community analysis, floristic assemblages, edge effects, fire-resistance functional traits, dispersal, population structures

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A mes Parents

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1 Préambule

1.1 Présentation du manuscrit / Overview of the manuscript

Cette thèse est composée d'une introduction et d'une conclusion générale rédigées en français et de trois chapitres intermédiaires rédigés en anglais et présentant les résultats. Chaque chapitre, composé d'articles acceptés, soumis ou en préparation et de matériels supplémentaires (résultats préliminaires n'ayant pas vocation à être soumis à publication en l'état), débute par un résumé en français. Les matériels et méthodes utilisés sont présentés dans chaque chapitre alors que toutes les références sont rassemblées à la fin de ce manuscrit.

This Ph.D. thesis consists of a general introduction and a general discussion written in French and three chapters presenting the results written in English. Each chapter is composed of scientific paper(s), which are submitted or in preparation, and supplementary materials (preliminary results, which are not intended to be submitted for publication in their present state). The materials and methods used are presented in each chapter while all cited references are listed at the end of this manuscript. Please refer to the section 2.5 for an English presentation of the objectives and the approaches used.

1.2 Contexte d'étude

Cette thèse s'intègre dans le projet Incendies et biodiversité des écosystèmes en Nouvelle-Calédonie (INC) financé par l'Agence Nationale de la Recherche (ANR-07-BDIV-008, début Janvier 2008 – fin Juin 2012) et coordonné par C. Hély.

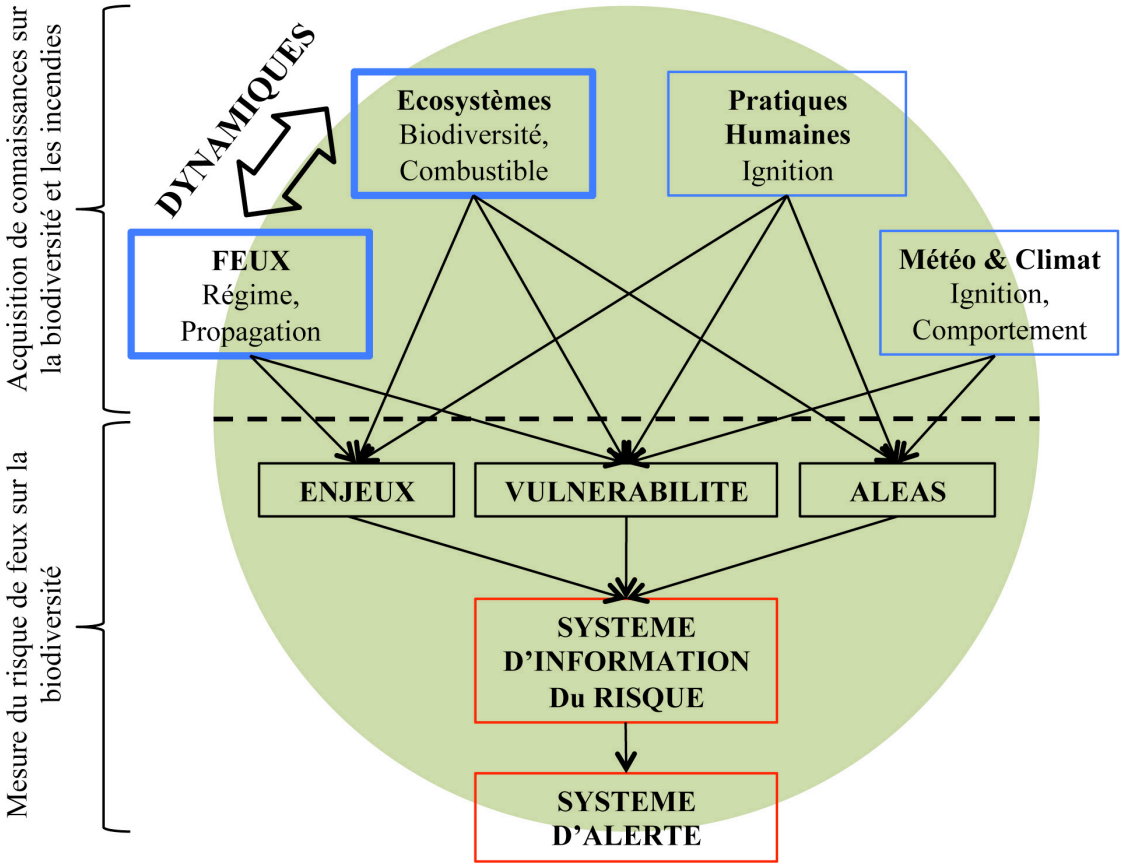


Figure 1.1 *La thèse au sein du projet INC. Le projet INC est divisé en deux parties, (i) acquisition de connaissances sur les feux, les écosystèmes, les pratiques humaines, la météorologie et la climatologie, et (ii) intégration des connaissances dans un SIG et développement d'un modèle décliné en un système d'information et un système d'alerte du risque de feux sur la biodiversité (les flèches représentent les interactions à analyser, modifié du projet INC, Hély 2007).*

Le projet INC analyse les interactions entre écosystèmes, pratiques humaines, climat et incendies, et développe un Système d'Information Géographique (SIG) pour suivre simultanément ces composantes dans l'espace et le temps (Figure 1.1). Ces composantes sont ensuite intégrées dans un Système d'Information (SI) combinant le SIG à un modèle de risque de feu sur la biodiversité néo-calédonienne. Ce SI sera décliné en un système d'alerte opérationnel pour l'aménagement du territoire en vue de la protection de la biodiversité face au risque de feu.

Au delà d'une participation à différentes composantes du projet INC impliquant plusieurs collaborations (e.g. Curt *et al.* in prep.; Hély *et al.* in prep.), cette thèse étudie les dynamiques de certains écosystèmes néo-calédoniens – savanes et forêts denses humides – en réponse aux incendies. C'est cette partie qui sera développée au long de ce manuscrit.

Au cours de cette thèse des sources de financement supplémentaires ont été obtenue *via* (i) un appel d'offre interne ECCOREV qui a permis la réalisation des travaux présentés dans le troisième chapitre de cette thèse (section 10 et 11) et le montage d'un stage en ethnoécologie (section 3.8.2) et, (ii) par une collaboration avec le WWF Nouvelle-Calédonie qui a permis la réalisation de travaux présentés dans le deuxième chapitre de cette (section 8).

2 Introduction générale

Cette thèse traite des dynamiques forestières – évolutions dans le temps et dans l'espace des compositions et des structures des populations et communautés qui constituent des espaces boisés, sous l'influence de facteurs naturels et/ou anthropiques – en Nouvelle-Calédonie. Plus précisément elle étudie les dynamiques des forêts denses humides et des savanes sous l'influence des incendies principalement d'origines anthropiques.

L'objectif de cette introduction générale est d'une part de replacer cette thèse dans un contexte global afin de mettre en avant les principaux enjeux liés à l'étude de ces dynamiques forestières et d'autre part de fournir un cadre théorique permettant d'aborder au mieux les travaux présentés.

2.1 Contexte global : Déforestation et crise de biodiversité

Fatigué de ces Hommes qui ont tué les indiens
Massacré les baleines, et bâillonné la vie
Exterminé les loups, mis des colliers aux chiens
Qui ont même réussi à pourrir la pluie
La liste est bien trop longue de tout ce qui m'écœure
Depuis l'horreur banale du moindre fait divers
Il n'y a plus assez de place dans mon cœur
Pour loger la révolte, le dégoût, la colère.

Renaud
Fatigué (Mistral gagnant, 1986)

Bien que les taux d'extinctions des espèces soient difficiles à évaluer, la biodiversité mondiale connait une crise majeure (Stork 2010). L'importance de cette crise de biodiversité est telle que certains écologues n'hésitent pas à parler d'une 'sixième crise d'extinction' (Barnosky *et al.* 2011; Stork 2010) en référence aux cinq extinctions de masse qui ont eu lieux au cours de l'histoire du vivant : à la fin de l'Ordovicien, du Dévonien, du Permien, du Trias et du Crétacé (Raup 1986). Contrairement à ces précédentes grandes crises, la crise actuelle de la biodiversité a une origine biologique et est le fait d'une seule espèce, l'Homme.

Cette crise de biodiversité est étroitement liée aux changements globaux d'origine anthropique parmi lesquels figurent les changements climatiques, les changements d'utilisations des terres ou encore l'augmentation de l'exploitation des ressources naturelles (voir Steffen *et al.* 2004 , pour un résumé complet des changements globaux). Outre le fait d'affecter la biodiversité, ces changements globaux affectent les services éco-systémiques (*e.g.* séquestration du carbone, régulation du

cycle de l'eau, fourniture de biens, rétention des sols) nécessaires au bien-être de l'Homme (Millenium Ecosystem Assessment 2005).

La perte d'habitats, leur fragmentation, et plus particulièrement la déforestation sont l'une des premières causes de perte de biodiversité (e.g. Brooks *et al.* 2002; Dirzo and Raven 2003; Millenium Ecosystem Assessment 2005). Selon la FAO (*Food and Agricultural Organisation of the United Nations*) environ 13 millions d'hectares de forêts ont été perdus au cours de la dernière décennie (pour une surface estimée de 4 milliards d'hectares en 2010), et bien que ce taux de déforestation soit en net recul par rapport aux années 90 (environ 16 millions d'hectares par an) il reste toujours alarmant (FAO 2010). Les forêts tropicales qui abritent plus des deux tiers de la biodiversité terrestre mondiale (Dirzo and Raven 2003; Gardner *et al.* 2009) sont les plus touchées (FAO 2010).

Le futur des forêts tropicales et de la biodiversité qu'elles abritent fait toutefois encore débat. Par exemple, la vision optimiste de Wright and Muller-Landau (2006a; b) liées au futur ralentissement de la démographie humaine mondiale et à l'urbanisation, a provoqué de vives réactions (Brook *et al.* 2006; Gardner *et al.* 2009; Gardner *et al.* 2007; Laurance 2007; Sloan 2007). En effet, il est difficile d'une part d'évaluer l'évolution des taux de déforestation et de reforestation, et d'autre part d'évaluer les réponses des espèces à ces changements en terme d'extinction (e.g. Brooks *et al.* 2002; Stork 2010). L'extinction des espèces met en jeux des processus écologiques complexes tels que les cascades écologiques (interactions entre les espèces, e.g. dispersion ou chaine trophique, Gardner *et al.* 2009) ou encore des effets d'extinctions à retardement (e.g. Brooks *et al.* 1999).

Les causes de déforestation sont multiples et synergiques comprenant à la fois des impacts anthropiques directs tels que l'exploitation forestière ou la conversion de forêts en zones agricoles mais aussi indirects *via* les changements climatiques, l'introduction d'espèces invasives ou encore la modification des régimes de perturbations (Gardner *et al.* 2009). Selon le *Secretariat of the Convention on Biological Diversity* (2001), les incendies sont devenus une menace croissante pour les forêts tropicales depuis le début des années 80 (voir Cochrane 2003). Cette menace s'est particulièrement illustrée lors de l'événement *El Niño* 1997-1998, le plus intense du 20ème siècle, car les incendies ont brulé environ 20 millions d'hectares de forêts

tropicales (Cochrane 2003; Nepstad *et al.* 1999; Siegert *et al.* 2001). Ces forêts tropicales, qui sont par nature peu exposées naturellement aux incendies, le sont désormais de plus en plus à cause de leurs fragmentations et de l'émergence de nouvelles pratiques d'utilisation du feu (Cochrane 2003; Goldammer 1999; Lewis 2006). Les changements de régimes de perturbations et la dégradation de la résilience des écosystèmes peuvent faire basculer ces écosystèmes forestiers dans un état alternatif comme les savanes avec des conséquences dramatiques pour la biodiversité (Folke *et al.* 2004; Scheffer *et al.* 2001; Scheffer and Carpenter 2003).

Bien que la crise de biodiversité soit un phénomène mondial, toutes les régions du monde ne sont pas égales en terme d'enjeux de conservation. En effet, la biodiversité et l'importance des menaces qui pèsent sur celle-ci ne sont pas également réparties dans le monde. Ainsi, certaines zones comme la Nouvelle-Calédonie présentent des enjeux majeurs, car elles abritent une exceptionnelle biodiversité associée à de fortes menaces. Etudier l'impact de perturbations anthropiques telles que les incendies sur les écosystèmes naturels qu'abritent ces zones est crucial pour la gestion et la conservation de la biodiversité.

2.2 La Nouvelle-Calédonie : Terre d'enjeux de conservation

« New Caledonia. My favorite Island : far enough off the east coast of Australia to spawn a unique fauna and flora ; large enough to accommodate large numbers of animals and plants ; and close enough to Melanesian archipelagoes to the north to have received elements from that different biogeographical realm. For the naturalist, New Caledonia is a melting pot and place of mystery. […] The New Caledonians, including the colonial French, have exploited the environment with abandon, logging, mining, and setting bush fires that push back the edges of the drier woodlands. […] To see New Caledonia as it was, you must climb to mountain slopes too remote or steep for the loggers to clear »

Edward O. Wilson
The Diversity of Life (1992)

2.2.1 Une exceptionnelle biodiversité

La Nouvelle-Calédonie est un archipel de 18500 km2 situé dans le sud-ouest du Pacifique juste au dessus du tropique du Capricorne, à 1500 km à l'est de l'Australie et 2000 kms au nord de la Nouvelle-Zélande. Elle est constituée d'une île principale, la Grande Terre (16500 km^2), des îles Belep au nord, de l'île des Pins au sud et des îles Loyauté à l'est.

La Nouvelle-Calédonie est depuis longtemps reconnue comme une zone de forts enjeux de conservation. Elle fait partie des dix premiers points chauds de diversité ou 'HotSpots' – zones présentant à la fois des concentrations d'espèces, des taux d'endémismes et des degrés de menace exceptionnels – décrits par Myers (1988), comme priorités pour la conservation de la biodiversité terrestre. Cette liste de zones prioritaires a depuis été élargie à 25 (Myers *et al.* 2000) et plus récemment à 34 zones (Mittermeier *et al.* 2004).

La Nouvelle-Calédonie est aussi l'un des rares territoires au monde à être à la fois une zone de conservation prioritaire pour la biodiversité terrestre et marine (Roberts *et al.* 2002). Ainsi elle abrite quatre des 238 écorégions – les Global 200 – définies à l'échelle mondiale comme priorités pour la conservation de, (i) ses forêts denses humides, (ii) ses forêts sèches, (iii) ses zones d'eau douce (rivières et fleuves) et, (iv) ses récifs coralliens (Olson and Dinerstein 2002). Selon ces mêmes auteurs, ces trois premières écorégions néo-calédoniennes, dont les forêts denses humides, sont considérées dans un état de conservation critique ou en danger alors que les récifs coralliens sont considérés dans un état relativement stable ou intact.

La Nouvelle-Calédonie est particulièrement reconnue pour la richesse de sa flore qui comprend à ce jour 3371 espèces dont 3099 plantes à fleurs (Morat *et al.* in prep.) et chaque année de nouvelles espèces continuent à être découvertes. Cette flore présente des taux d'endémisme exceptionnels : 74,4 % pour l'ensemble de la flore (3ème rang mondial) et 77,8 % pour la flore des plantes à fleurs (angiospermes). Les taux d'endémismes atteignent même 87,4 % et 92,1 % pour la flore des plantes à fleurs des forêts denses humides et des maquis. La Nouvelle-Calédonie se démarque aussi par ses nombreux cas de micro-endémisme (e.g. Bradford and Jaffre 2004; Pillon and Nooteboom 2009).

« Nos botanistes ne se plaignaient pas d'être inoccupés, car chaque jour apportait à la botanique ou aux autres branches de l'histoire naturelle quelque objet nouveau. »

James Cook (1774)
Traduit de l'anglais par G. Rives
Relations de voyages autour du monde

L'originalité de la flore néo-calédonienne ne se limite pas à son fort endémisme. En effet elle comprend notamment de nombreuses plantes primitives telles que *Amborella trichopoda*, unique représentant actuel des *Amborellaceae*, endémique à la Nouvelle-Calédonie, et qui est le *taxon* le plus basal de l'arbre phylogénétique des

plantes à fleurs (Jansen *et al.* 2007; Soltis *et al.* 2000). La Nouvelle-Calédonie abrite aussi une grande variété de conifères (voir Jaffre *et al.* 2010) tels que les *Araucaria* (dont l'emblématique pin colonnaire, *A. columnaris*) et les *Agathis* ou 'kaoris' de la famille des *Araucariaceae*, ou encore la seule espèce de gymnosperme parasite connue au monde, *Parasitaxus usta* (*Podocarpaceae*).

La particularité et la richesse de sa flore et l'origine Gondwanienne de la Nouvelle-Calédonie, font d'elle un véritable 'laboratoire' pour les taxonomistes et évolutionnistes (Murienne 2009). La Nouvelle-Calédonie a une histoire géologique particulière puisqu'elle s'est détachée du Gondwana il y 83 Ma avant d'avoir été submergée pendant plus de 20 Ma (voir Grandcolas *et al.* 2008). Ainsi différentes hypothèses ont été émises pour expliquer les origines, la diversification et l'évolution de la flore néo-calédonienne (Grandcolas *et al.* 2008; Murienne 2009; Murienne *et al.* 2005).

2.2.2 Diversité éco-systémique

Cette exceptionnelle biodiversité est portée par une mosaïque d'écosystèmes liés aux différents types de sols (ultramafique, volcano-sédimentaire ou calcaire), aux gradients de précipitation, au fort relief et aux différentes activités humaines (Jaffré 1993; Jaffré *et al.* 2009; Jaffré and Veillon 1994). D'un point de vue de conservation, cinq grands types de végétation ont été définis par Jaffré *et al.* (1998), (i) la forêt dense humide, (ii) la forêt sèche ou sclérophylle, (iii) le maquis de basse et de moyenne altitudes (< 900 m), (iv) le maquis de haute altitude (> 900 m), et (v) les formations secondaires (anthropiques) ; savanes à niaoulis (*Melaleuca quinquenervia*) et fourrés à gaïac (*Acacia spirorbis*) ou à faux-mimosa (*Leucaena leucocephala*) qui ont une faible valeur de conservation. A ces cinq catégories, il faut toutefois ajouter les végétations de zones humides telles que les mangroves (Figure 2.1).

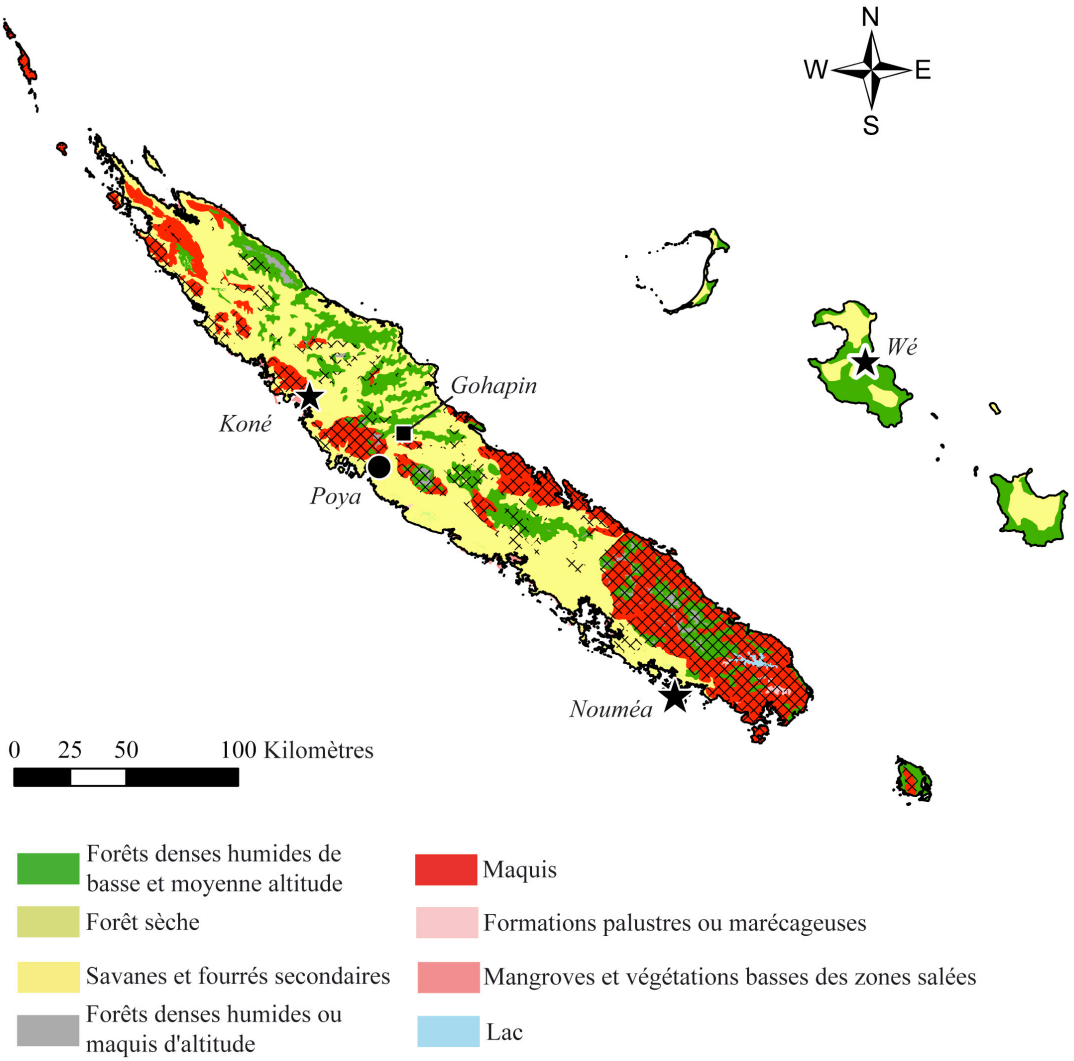


Figure 2.1 *Carte simplifiée de la végétation de la Nouvelle-Calédonie (modifiée de l'Atlas de Nouvelle-Calédonie). Les zones hachurées représentes les sols ultramafiques et serpentineux.*

2.2.3 Perturbations et évolution de la végétation néo-calédonienne

Afin de mieux comprendre les paysages actuels et les dynamiques de végétations qui y sont associées, il est important de connaître leurs histoires et celle des perturbations anthropiques qui ont causé leurs évolutions. Ceci semble d'autant plus important que les paysages actuels sont le résultat d'une anthropisation relativement récente (Figure 2.2).

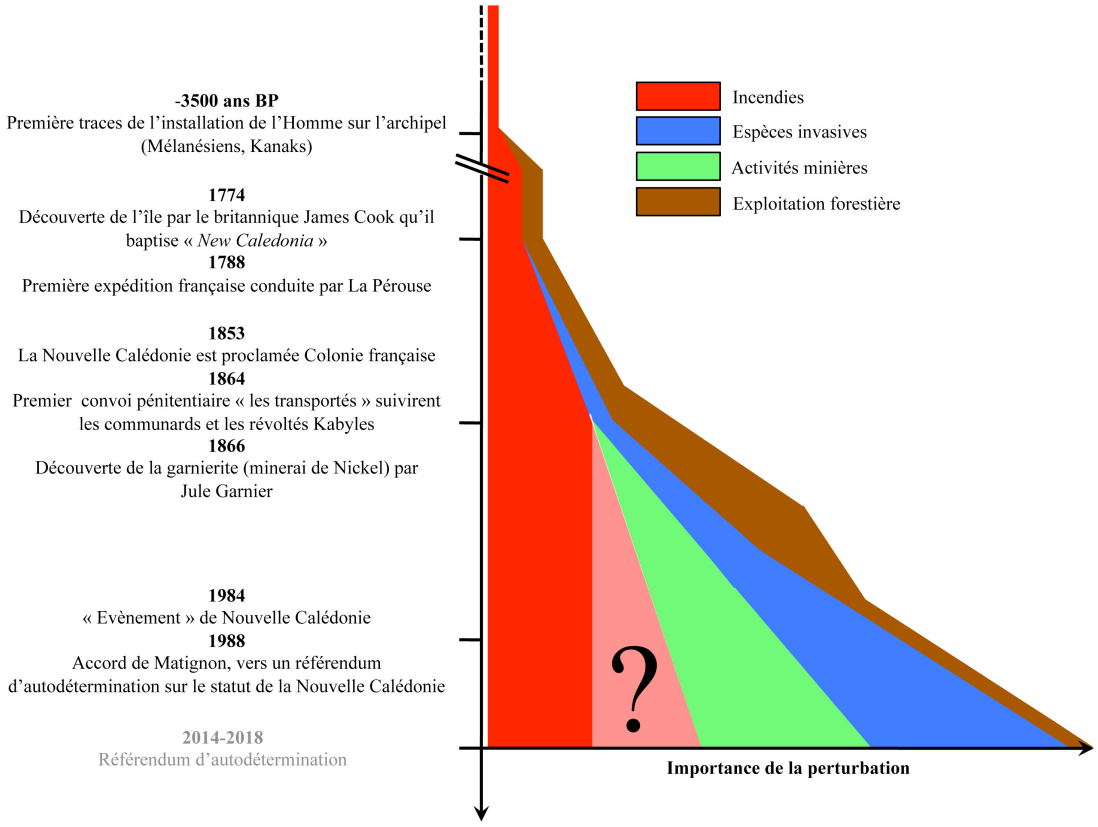


Figure 2.2 *Histoire simplifiée de la Nouvelle-Calédonie et évolution des perturbations anthropiques. L'importance des perturbations n'est pas basée sur des données chiffrées mais reflètes les tendances trouvées dans la littérature. Le point d'interrogation note l'incertitude sur l'évolution (zone saumon) de l'importance des incendies.*

Les enregistrements paléo-écologiques (Hope and Pask 1998; Stevenson 2004) et l'étude de la biogéographie des formations naturelles (Jaffré *et al.* 1998) montrent que la végétation néo-calédonienne a considérablement été modifiée depuis l'installation de l'Homme sur l'archipel il y a environ 3500 ans. Selon Jaffré *et al.* (1998), plus de la moitié de la surface des formations naturelles néo-calédoniennes a

déjà disparu. Toutefois, cette dernière estimation devrait certainement être revue à la hausse aujourd'hui.

Les enregistrements paléoécologiques montrent que les incendies naturels (initiés par la foudre) semblent avoir existé longtemps avant l'arrivée de l'Homme, cependant leur fréquence a augmenté avec l'établissement des Mélanésiens sur l'île (Hope and Pask 1998; Stevenson 2004; Wirrmann *et al.* 2006). Selon ces derniers auteurs, cette augmentation des feux vue par les charbons dans les sédiments coïnciderait avec l'enregistrement au niveau des pollens graminéens des premières savanes dans les paysages néo-calédoniens.

Avec l'arrivée des premiers Européens (découverte de l'île par James Cook en 1774) et surtout depuis la colonisation Française de l'île (1850), la modification du paysage s'est certainement accélérée, d'une part à cause de l'augmentation de la fréquence des incendies, vraisemblablement utilisés pour ouvrir le milieu, et d'autre part par l'introduction de nouvelles perturbations. Ainsi, l'exploitation des ressources naturelles, principalement forestières, s'est développée avec l'arrivée des premiers bagnards (Sebert 1874). La Nouvelle-Calédonie n'est cependant pas un territoire forestier et cette exploitation difficile et peu rentable restera par la suite faible (Sarlin 1954). De plus, l'augmentation de la population liée à la colonisation a certainement aussi été à l'origine d'une grande ouverture du milieu et notamment de la destruction des forêts sèches au profit de prairie ou de pâturage pour l'élevage extensif du bovin (aujourd'hui encore très répandu) et de savanes (Sarlin 1954; Virot 1956). Ces formations couvrent aujourd'hui la majeure partie de la côte ouest de la Nouvelle-Calédonie alors que les forêts sèches n'occupent que 1 % de leur surface originelle (Gillespie and Jaffré 2003).

La découverte de la garniérite (minerai de Nickel) en 1866 et son exploitation a profondément modifié les paysages sur les sols métallifères (ultramafiques). La prospection, l'exploitation à ciel ouvert et l'utilisation des incendies pour ouvrir le milieu sont certainement en grande partie à l'origine de la réduction et de la fragmentation des forêts denses humides sur sols ultramafiques, mais aussi de la dégradation des maquis. La Nouvelle-Calédonie abrite près d'un quart des réserves mondiales en nickel. Aujourd'hui son exploitation, qui est en plein essor (ouverture de nouvelles mines), est la principale source de richesse du territoire.

Enfin, l'introduction d'espèces exogènes végétales et animales, souvent nuisibles et invasives, constitue la dernière grande perturbation anthropique qu'a vu apparaître la Nouvelle-Calédonie. Les îles tropicales sont particulièrement vulnérables à ces introductions (Denslow 2003; Sherley 2000). En Nouvelle-Calédonie elles ont débuté dès l'arrivée des Mélanésiens mais se sont surtout développées lors de la colonisation européenne et ont connu une forte augmentation depuis les années 1950 (Gargominy *et al.* 1996). Un récent rapport porte au nombre de 1847 le nombre de *taxons* végétaux introduits parmi lesquels, 597 sont spontanés et 200 sont invasifs (e.g. *Leucaena leucocephala*, *Lantana camara*, *Melinis minutiflora* ou *Pinus caribaea* var. *hondurensis*) ou le sont potentiellement (Hequet *et al.* 2009). Parmi les espèces animales les plus répandues et les plus nuisibles, on trouve les rats (*Rattus spp.*), le cochon (*Sus scrofa*) et le cerf rusa (*Cervus timorensis russa*).

L'impact de ces espèces invasives est multiple, à la fois direct (compétition avec les communautés autochtones (e.g. Denslow *et al.* 2006; Hoffmann and Haridasan 2008; Hooper *et al.* 2005), prédation (e.g. De Garine-Wichatitsky *et al.* 2005) et indirect avec par exemple la modification des régimes d'incendies (e.g. Hoffmann *et al.* 2004; Mack and D'Antonio 1998; Mistry and Berardi 2005).

Aujourd'hui, les principales perturbations anthropiques affectant les formations végétales néo-calédoniennes et menaçant la biodiversité qu'elles abritent sont les activités minières, les incendies et les espèces invasives (Jaffré *et al.* 1998; Pascal *et al.* 2008). Les incendies touchent l'ensemble des formations alors que les activités minières touchent principalement les formations végétales sur substrats ultramafiques (présence de nickel) et les espèces invasives plutôt celles sur substrats volcano-sédimentaires (Hequet *et al.* 2009).

2.2.4 Les différentes formations forestières et les dynamiques associées

Comme suggéré précédemment, différents types de formations forestières sont distingués en Nouvelle-Calédonie en fonction de la quantité de précipitation et du substrat sur lequel elles poussent. Ainsi on distingue : (i) les forêts sèches ou forêts sclérophylles (50 km^2), situées en dessous de 300 m d'altitude sur substrats volcano-sédimentaires dans les zones recevant moins de 1000 mm de précipitation par an, (ii) les forêts denses humides sur substrats volcano-sédimentaires (1800 km^2), (iii) les forêts denses humides sur substrats ultramafiques (1100 km^2) et (iv) les forêts denses humides sur substrats calcaires (900 km^2). Ces différentes formations partagent un certain nombre d'espèces, mais présentent toutefois des assemblages floristiques différents (Jaffré *et al.* 2009; Jaffré *et al.* 2008; Jaffré and Veillon 1995; Jaffré *et al.* 1997a). Par exemple, selon Jaffré *et al.* (1997a) 39,6 % et 43,8 % de la flore des forêts denses humides sur substrats volcano-sédimentaires et ultramafiques leur sont exclusifs. De plus, Jaffré et Veillon (1995) ont montré que les *taxa* dominant ces deux formations ne sont pas les mêmes.

Sur l'île principale de la Nouvelle-Calédonie (la Grande Terre), les formations secondaires (anthropiques) associées aux forêts sèches et aux forêts denses humides sur substrats volcano-sedimentaires sont principalement les savanes et les fourrés secondaires qui recouvrent plus de 35 % du territoire (6000 km^2). De la même façon, les formations secondaires associées aux forêts denses humides sur substrats ultramafiques sont les formations para-forestières (e.g. formations à *Gymnostoma deplancheanum*) et les maquis (4600 km^2). Cependant ces maquis comprennent à la fois des formations secondaires mais aussi des formations naturelles (ou 'climaciques') liées au type de sol.

De part leurs originalités, les maquis et les forêts denses humides sur substrats ultramafiques ainsi que leurs dynamiques liées aux incendies sont de loin les formations les plus étudiées en Nouvelle-Calédonie (Enright *et al.* 1999; Enright *et al.* 2001; McCoy *et al.* 1999; Perry and Enright 2002a; b; Perry *et al.* 2001; Rigg *et al.* 2002). Les forêts sèches, étant l'une des formations les plus menacées à l'échelle mondiale (Wright and Muller-Landau 2006a) et la plus menacée à l'échelle de la Nouvelle-Calédonie (Gillespie and Jaffré 2003), ont aussi fait l'objet de quelques études notamment à travers le développement du programme d'étude des forêt sèches

(http://www.foretseche.nc/). Cependant peu de publications existent à notre connaissance sur leurs dynamiques (Bocquet *et al.* 2007).

Les dynamiques des forêts denses humides sur substrats volcano-sedimentaires, bien qu'étant les plus importantes en terme de superficie, restent très peu étudiées. Avant ces travaux de thèse, aucune publication à notre connaissance, n'y faisait référence. Même dans le document le plus complet concernant l'impact des incendies sur la végétation néo-calédonienne (Jaffré *et al.* 1997b), seuls les cas des forêt sèches et des forêts denses humides sur substrats ultramafiques ont été traités.

Cette thèse, en se focalisant sur les dynamiques forêts denses humides – savanes, ouvre ainsi un nouveau champ de recherche en Nouvelle-Calédonie. Outre l'étude des processus écologiques mis en jeu lors de l'expansion et de la contraction forestière, liés au régime et au comportement des incendies, cette thèse fournit une première description des communautés végétales caractérisant les différents stades de ces dynamiques.

2.3 Forêt dense humide – savane : cadre théorique

2.3.1 Biogéographie

Les forêts denses humides et les savanes tropicales se partagent environ un quart de la surface terrestre (environ 6 % et 20 %, respectivement) et recouvrent à peu près 20 % (tous types confondus) et 30 % de la Nouvelle-Calédonie (Jaffré *et al.* 2009). Ce sont deux écosystèmes très différents en termes de composition, de structure, de fonctionnement mais aussi d'inflammabilité. Les savanes sont en effet principalement caractérisées par une couche herbacée continue avec un couvert arboré discontinu (Scholes and Archer 1997). Récemment, dans '*When is a 'forest' a savanna, and why does it matter ?*' (Ratnam *et al.* 2011), les savanes tropicales sont décrites comme étant des écosystèmes caractérisés par la coexistence d'arbres et d'herbacées en C4, et constitués d'espèces tolérantes aux incendies et intolérantes à l'ombrage, alors qu'à l'inverse dans les forêts, les herbacées en C4 sont absentes et les espèces sont

intolérantes aux incendies et tolérantes à l'ombrage. Ainsi pour qu'une savane existe et perdure, il faut que les herbacées et les arbres puissent coexister *via* la limitation du couvert arboré (Bond 2008).

Différents facteurs peuvent limiter synergiquement le couvert arboré en savane. Bond (2008) classe ces facteurs en deux catégories, (i) les facteurs qui contrôlent le couvert arboré par la ressource (*Bottom-Up*) que représente la disponibilité en eau et en nutriments, et (ii) ceux qui le contrôlent par la prédation (*Top-Down*) ; le pâturage et les incendies (voir, Bond and Keeley 2005; Midgley *et al.* 2010; van Langevelde *et al.* 2003, pour plus d'informations). La ressource est principalement la disponibilité en eau (*i.e.* les précipitations) et elle semble limiter le couvert arboré potentiel, alors que les perturbations tels que le pâturage et les incendies font plus ou moins s'éloigner le couvert arboré de son potentiel maximum (Bucini and Hanan 2007; Sankaran *et al.* 2005; Sankaran *et al.* 2004; Staver *et al.* 2011a).

Ainsi suivant la quantité de précipitation, la savane ou la forêt peuvent être comme en Nouvelle-Calédonie, deux états alternatifs stables, qui peuvent passer de l'un à l'autre en fonction du régime de perturbations (Scheffer and Carpenter 2003; Schroder *et al.* 2005; Staver *et al.* 2011a; Warman and Moles 2009). Cette hypothèse a récemment été renforcée à l'échelle globale par Hirota *et al.* (2011) en confrontant des données de couvertures arborées et de précipitations en Afrique, Australie et Amérique du Sud. A partir du même jeu de données de couvertures arborées, Staver *et al.* (2011b) mettent en avant le rôle crucial que jouent les incendies dans la distribution globale des savanes et forêts dans les zones où les précipitations annuelles sont comprises entre 1000 et 2500 mm (Figure 2.3). En effet, dans ces zones les savanes fortement inflammables du fait de la présence importante de combustible herbeux sec, favorisent les incendies qui en retour maintiennent les savanes ouvertes en empêchant l'établissement de ligneux. Ces processus de rétroaction positive permettent la coexistence de savanes et de forêts denses humides dans un même paysage (Figure 2.4).

Ainsi, comme le suggèrent Jaffré *et al.* (1998) et en accord avec les résultats de Staver *et al.* (2011b), au vu du régime de précipitation (Figure 2.5) les savanes néo-calédoniennes sont des formations purement liées aux perturbations résultants de la limitation du couvert arboré par le pâturage et les incendies anthropiques. Le pâturage

peut être considéré comme un facteur majeur permettant le maintien des savanes sur la côte ouest de la Nouvelle-Calédonie et à basse altitude, car l'élevage extensif de bovins y est très répandu. Cependant, dans le reste de l'île et notamment le long de la chaîne de montagne centrale l'élevage est très peu développé et l'hypothèse que les incendies soient le principal facteur permettant le maintient des savanes est raisonnable. Dans ces zones, selon la fréquence des incendies, les forêts et les savanes se côtoient et peuvent représenter deux états alternatifs stables pouvant basculer d'un état à l'autre si une composante du régime de perturbation (fréquence, intensité…) vient à changer (Figure 2.3).

Les incendies semblent donc affecter de deux façons les dynamiques des forêts denses humides et des savanes en Nouvelle-Calédonie. En effet, d'une part les incendies permettraient l'avancée des savanes en érodant les formations forestière (Jaffré *et al.* 1997b) et d'autre part, ils permettraient de maintenir la savane ouverte en limitant l'installation d'arbres forestiers.

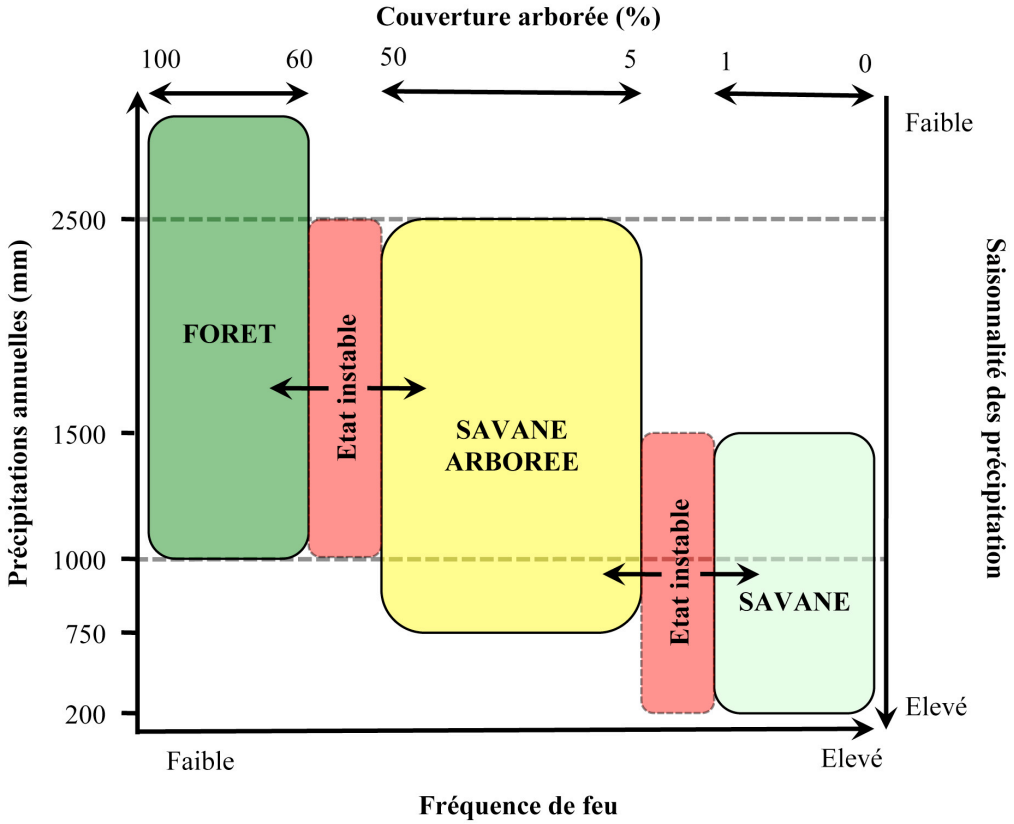


Figure 2.3 *Distribution des forêts denses humides et des savanes en fonction des précipitations annuelles et de la fréquence de feu (modifié de Mayer and Khalyani 2011).*

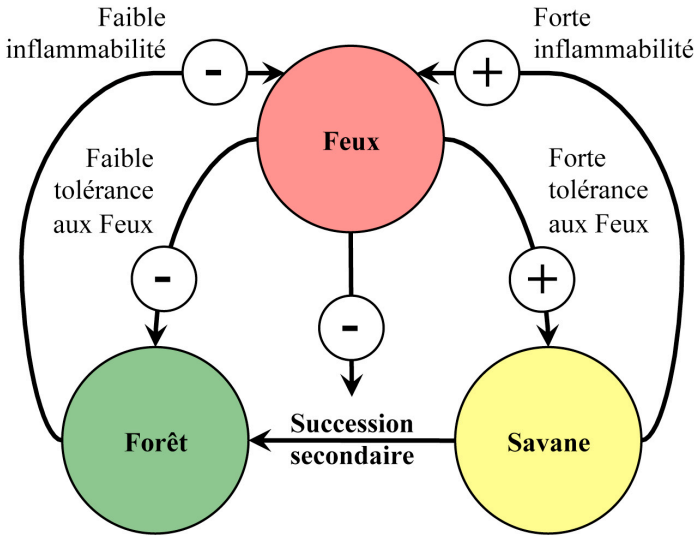


Figure 2.4 *Boucles de rétroactions permettant le maintient des savanes et des forêts dans un même paysage*

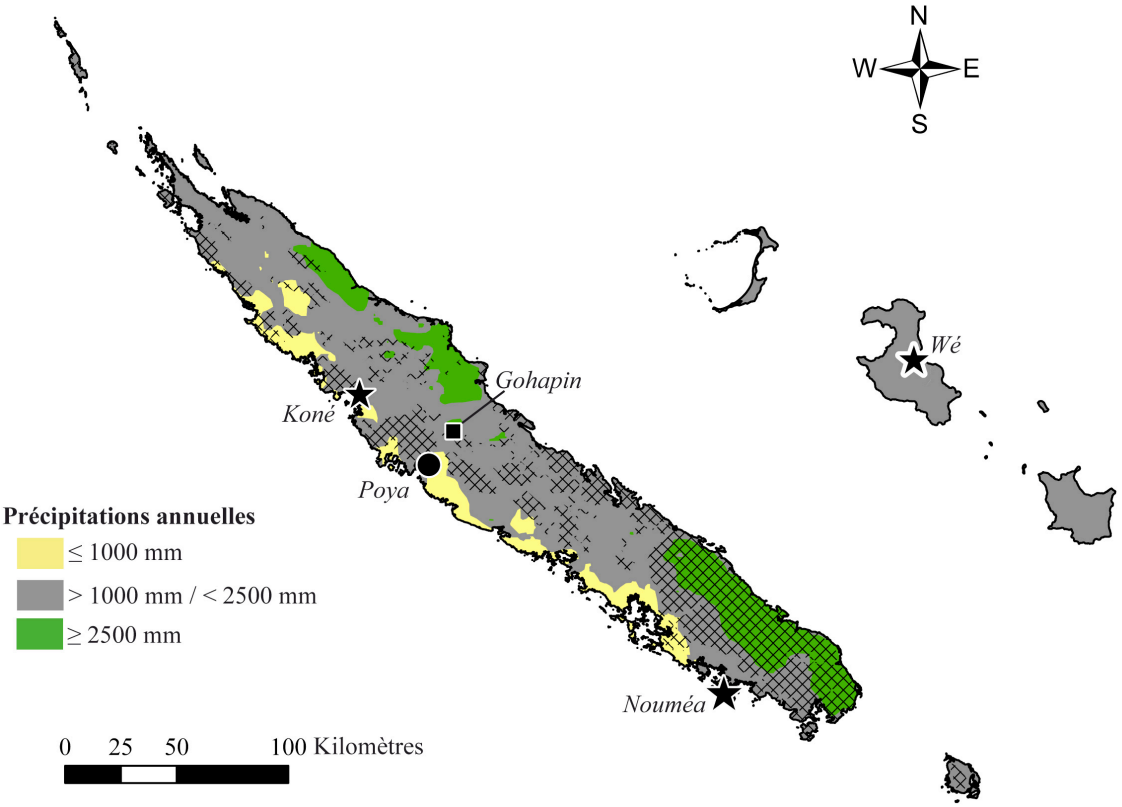


Figure 2.5 *Carte des précipitations annuelles. La zone grise (précipitations comprises entre 1000 et 2500 mm par an) hors zone hachurée (correspondant aux substrats ultramafiques et serpentineux), représente la zone ou les savanes et les forêts denses humides peuvent être deux états alternatifs stables (voir* Figure 2.3*). Carte réalisée à partir des données de l'Atlas de Nouvelle-Calédonie.*

2.3.2 Les incendies : bases théoriques

Les incendies – feux ou combustions non maitrisés dans le temps et dans l'espace – affectent à différentes échelles spatiales et temporelles les dynamiques des forêts denses humides et des savanes (Figure 2.6). L'impact des incendies sur la végétation ou plus largement sur un écosystème donné dépend de leurs régimes et notamment de la composante comportement.

Le but de cette section est de fournir un cadre théorique non exhaustif sur l'écologie du feu (combustion, comportement, régime et impact sur la végétation) afin de mieux comprendre la démarche suivie dans cette thèse et les résultats présentés. Pour plus d'informations, Whelan (1995) a rédigé un ouvrage complet sur l'écologie du feu, et plus récemment, Stott (2000) a fourni une synthèse sur les processus de combustion en milieu tropical.

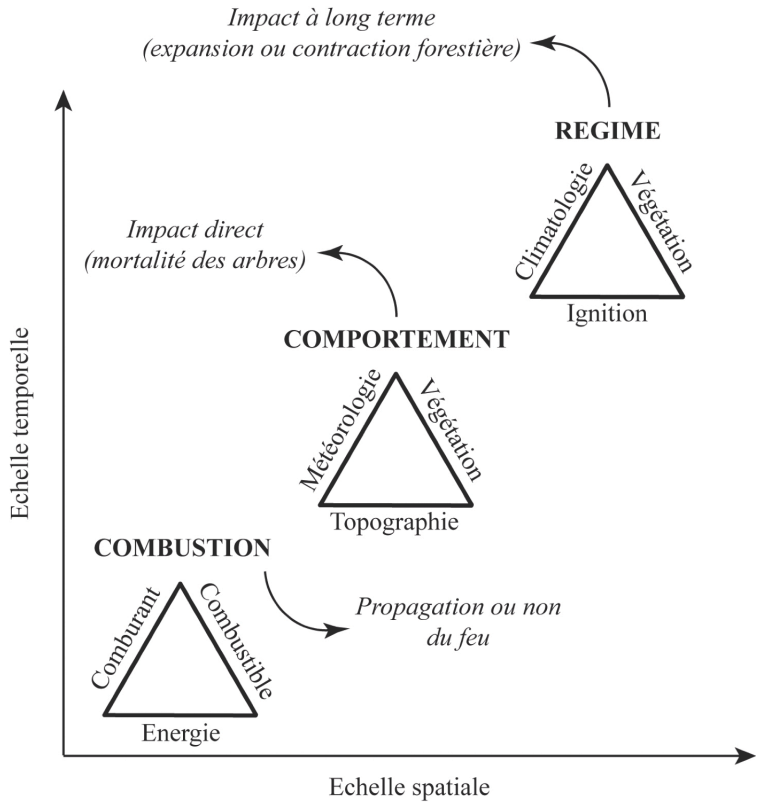


Figure 2.6 *Interactions entre les principaux facteurs caractérisant l'écologie du feu à différentes échelles spatiales et temporelles.*

Combustion et propagation du feu

La combustion est une réaction chimique d'oxydation exothermique au cours de laquelle l'énergie emmagasinée lors de la photosynthèse est libérée sous forme de chaleur (Whelan 1995). C'est cette énergie, qui transmise à la végétation par conduction, convection ou radiation, peut induire la nécrose des tissus végétaux et *in fine* la mort d'individus (Figure 2.7). Un feu est donc une suite de combustions qui opèrent de proche en proche permettant au feu dans la phase de flamme de se déplacer spatialement (propagation). Une synthèse complète de ces processus de transfert d'énergie est proposée par Michaletz and Johnson (2007).

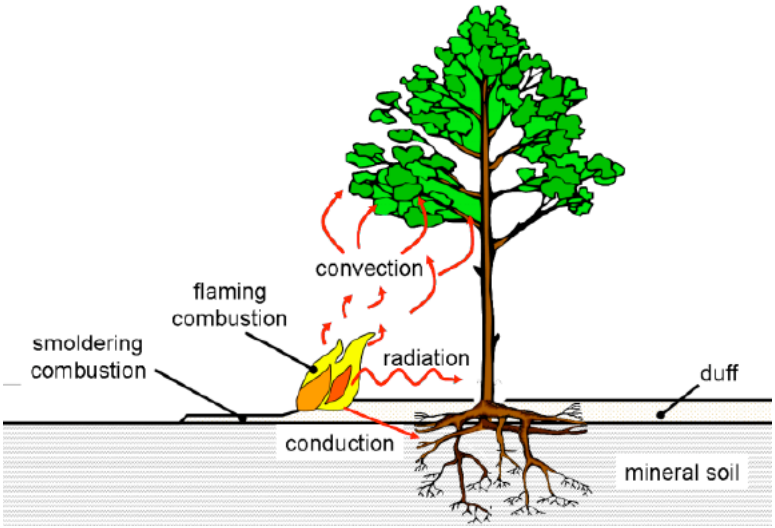


Figure 2.7 *Processus de transferts de chaleur depuis la combustion vers un arbre (tiré de Michaletz and Johnson 2007).*

La combustion ne peut se produire qu'en présence et dans les bonnes proportions de trois éléments (le triangle du feu) ; combustible, comburant (oxygène) et énergie d'activation. Si à un moment ou à un autre, l'un de ces trois éléments fait défaut, la combustion s'arrête et le feu s'éteint ; dans le cas contraire, la combustion se propage de proche en proche. L'inflammabilité d'un combustible, c'est à dire sa capacité à prendre feu quand il est exposé à une source d'énergie, mais aussi sa capacité à entretenir la combustion, dépend principalement de son humidité. Cette dernière dépend des conditions météorologiques, mais aussi de la taille du combustible (les

combustibles les plus fins tels que les herbes se desséchant plus vite que les plus volumineux tels que les branches ou les troncs) et de son statut (le matériel végétal vivant se desséchant moins rapidement que du matériel mort qui est en 'équilibre' avec les conditions météorologiques). Ainsi, les savanes qui présentent une couche herbacée continue se desséchant rapidement lors des périodes sèches sont très inflammables (Hély and Alleaume 2006) contrairement aux forêts denses humides (Stott 2000).

Comportement du feu

Tant que les bonnes conditions de combustion sont réunies, le feu se propage grâce à l'avancement de la flamme. Le comportement du feu (i.e. les caractéristiques de sa propagation), détermine son impact potentiel à court terme sur la végétation. Le comportement d'un feu est principalement caractérisé en terme de type (feu de surface et / ou de couronne), de vitesse de propagation ($m.s^{-1}$) ou de temps de résidence (s), de longueur et de hauteur de flamme (m), d'intensité (i.e. la quantité de chaleur ou d'énergie émise par la combustion, exprimée en $kW.m^{-2}$) et de profondeur (m) du front de flamme. Le temps de résidence, l'intensité et la profondeur du front de flamme déterminent la quantité d'énergie transférée par le feu, alors que le type de feu et la hauteur de flamme (qui dépend de l'intensité du feu, de la topographie et du vent) déterminent quelles parties de la végétation y sont exposées (e.g. Michaletz and Johnson 2006; Van Wagner 1973).

Les principaux facteurs dirigeant le comportement d'un feu sont la topographie, la météorologie (température, humidité et vitesse du vent) et la végétation. La topographie influence l'humidité et l'exposition au vent et peu constituer des coupes feux. La pente favorise la propagation du feu en rapprochant le front de flamme du combustible non brûlé en amont et en favorisant sa dessiccation par radiation (Figure 2.8). Le vent, en couchant la flamme a un effet similaire (Figure 2.8), et de plus il favorise la combustion en augmentant l'apport de comburant (oxygène). La température et l'humidité de l'air quant à eux définissent à long terme la disponibilité de combustible à travers l'état de dessiccation du combustible avant le feu. Enfin les précipitations sont le principal facteur de la production de combustible notamment herbeux en milieu tropical (Hély and Alleaume 2006). La végétation définit le lit de

combustible selon son type, sa quantité et son arrangement spatial. Un continuum horizontal du combustible permet la propagation du feu dans une strate de végétation donnée et le continuum vertical permet son passage d'une strate à une autre (e.g. de la surface vers la couronne des arbres).

Finalement, la sévérité d'un incendie – son impact réel – sur l'écosystème et notamment sur la végétation dépend à la fois de son comportement mais aussi de la tolérance aux incendies de cette végétation (Keeley 2009). Ainsi les feux de savane sont souvent peu sévère car la végétation y est adaptée, alors que les feux se propageant dans le sous-bois des forêts denses humides, bien que moins intense, ont une sévérité plus élevée étant donné que les essences forestières sont peu tolérantes aux incendies (e.g. Hoffmann *et al.* 2003; Nepstad *et al.* 1999).

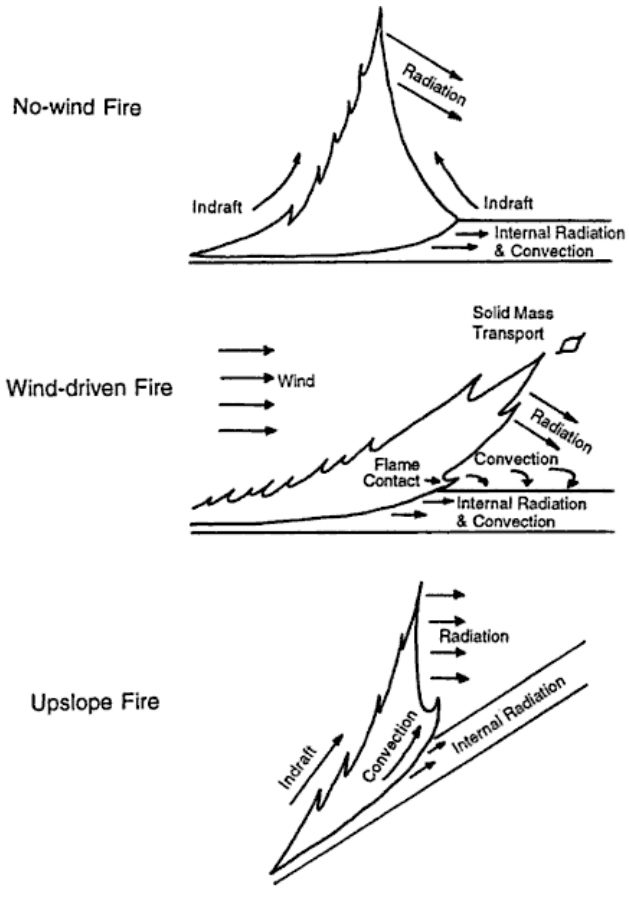


Figure 2.8 *Influences similaires du vent et de la topographie sur le comportement du feu (tiré de Alexander 1982).*

Régime d'incendies

L'effet des incendies à long terme sur les écosystèmes et leurs dynamiques (*i.e.* expansion ou contraction forestière) dépend de leurs régime (e.g. Franklin *et al.* 2001; Liedloff and Cook 2007; McCoy *et al.* 1999; Perry and Enright 2002a; b; Perry *et al.* 2001). Le régime d'incendie d'un écosystème s'articule autour de trois composantes (temporelle, spatiale et amplitudinale, voir Hély and Alleaume, 2006) et qui définissent les caractéristiques des feux qui surviennent généralement sur un territoire donné ou pour un écosystème donné. Chaque composante se définit elle-même à partir de plusieurs variables. La composante temporelle inclut la saison des feux, la fréquence des feux (nombre de feux ou proportion de territoire brûlé par unité de temps), l'intervalle de feu (temps entre deux feux successifs au même endroit) et le cycle de feu (temps pour qu'une superficie équivalente à la zone étudiée soit brûlée). La composante spatiale prend en considération la taille et le type de feux et la composante amplitudinale correspond aux variables du comportement du feu (vitesse, intensité) en lien avec la sévérité à long-terme sur la régénération de la végétation. Les principaux facteurs déterminant les caractéristiques de ce régime sont le climat, la végétation et l'ignition. Le climat est le facteur le plus important et il agit à différentes échelles temporelles sur le régime d'incendie. A grande échelle, il influence le type de végétation et à une échelle plus fine il détermine la quantité et l'humidité du combustible, et les conditions météorologiques avant et pendant la propagation des feux.

Le climat Néo-Calédonien est tropical océanique avec une saison fraiche (de Juin à Septembre) et une saison chaude (d'Octobre à Mai), toute deux chevauchées par une saison sèche caractéristique d'Août à Novembre. Cette saison sèche, qui correspond à la saison des feux de brousse, est caractérisée par une faible pluviométrie, une hausse des températures, et des vents d'est (les Alizés) soufflant régulièrement. La variabilité interannuelle du climat néo-calédonien (longueur et intensité de la saison sèche) est principalement dirigée par l'oscillation Australe *El Niño* (ENSO, Ropelewski and Halpert 1987). Pendant les évènements *El Niño* la pluviométrie diminue (50% de sa valeur habituelle), alors que pendant les évènements *La Niña* la tendance inverse est observée (Delcroix and Lenormand 1997; Nicet and Delcroix 2000).

Si les conditions sont réunies pour la propagation d'un incendie, c'est l'ignition qui détermine si l'incendie aura lieu ou non. Le climat joue donc un rôle prépondérant dans la fréquence des incendies lorsque les ignitions sont d'origines naturelles (foudre). Cependant dans de nombreux écosystème tropicaux (Stott 2000) comme en Nouvelle-Calédonie (Jaffré *et al.* 1998; Jaffré *et al.* 1997b) les ignitions sont le plus souvent d'origine anthropique. Les activités humaines sont alors un facteur déterminant dans la fréquence des incendies.

La fréquence des incendies et les intervalles de feu sont particulièrement importants dans les dynamiques des savanes et des forêts denses humides. Une fréquence d'incendies relativement élevée ou un intervalle cours permettent le maintien des savanes alors qu'une fréquence faible ou un intervalle long permettent l'installation et le développement d'arbres induisant l'expansion forestière.

2.3.3 Les incendies en Nouvelle-Calédonie

Bien que les incendies soient considérés comme l'une des principales menaces pour la biodiversité en Nouvelle-Calédonie, leurs comportements ou leur régime sont très peu documentés. Combler ce manque de connaissance était l'un des principaux objectifs du projet ANR INC (ANR-07-BDIV-008) dans lequel s'est intégrée cette thèse.

Un premier historique des feux sur la période 1999-2010 a ainsi pu être fourni à partir de produit de télédétection MODIS et Landsat (Curt *et al.* in prep.). Au cours de cette période, 583 feux (de 2 à 3641 ha) ont été détectés pour une surface totale de 29427 ha (soit environ 2 % de la surface de l'île principale, Figure 2.9). Cependant cet historique est loin d'être exhaustif: d'une part les petits feux (< 2 ha) ne sont pas détectés et d'autre part les feux de surface en sous-bois forestiers, s'ils peuvent exister, ne sont pas non plus détectés. Bien que cet historique sous-estime la menace portée par les incendies sur la biodiversité néo-calédonienne, il met en avant l'importance des feux de savanes dans les dynamiques des forêts denses humides. En effet, selon cette étude, les savanes comptent parmi les écosystèmes néo-calédoniens qui brûlent le plus et 64 % des feux initiés en savane atteignent la lisière de forêts denses humides (Curt *et al*. in prep.).

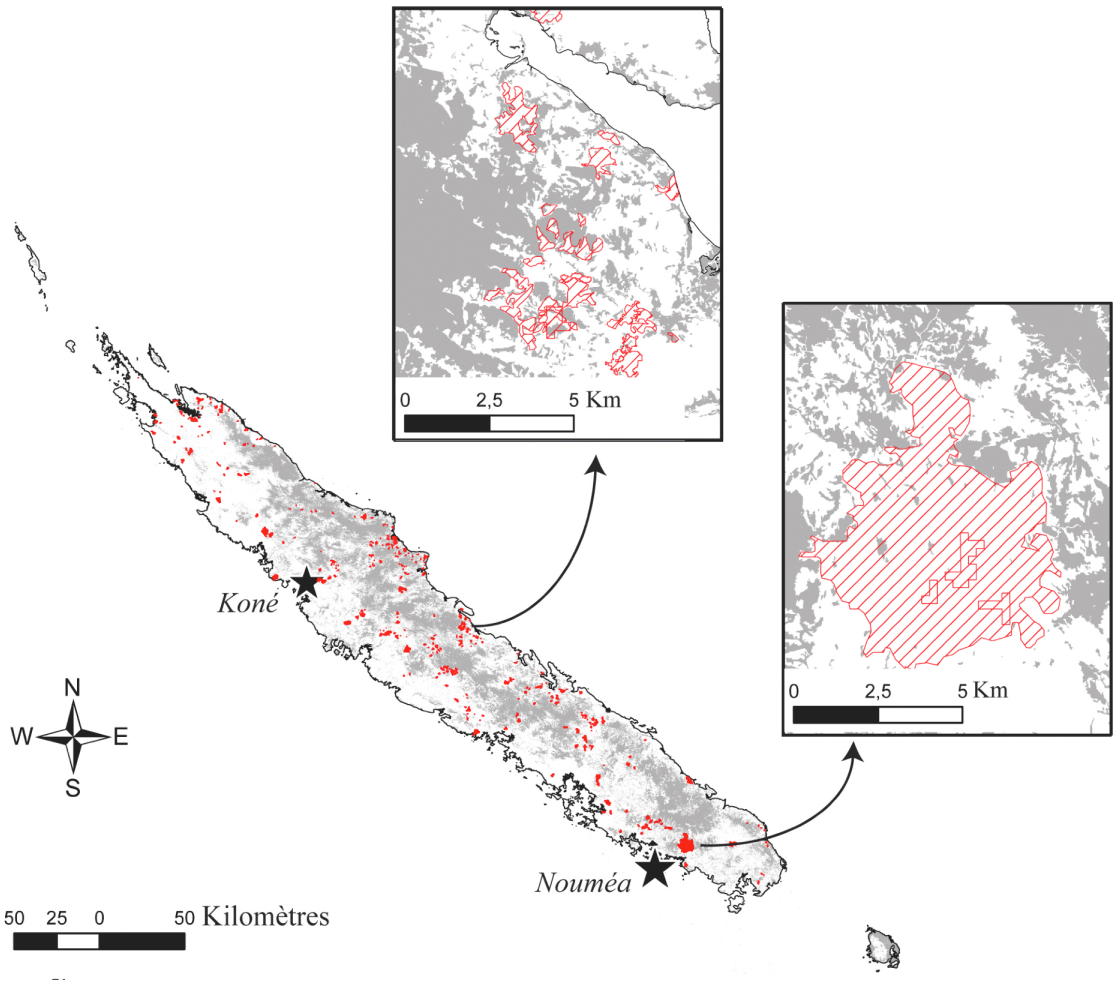


Figure 2.9 *Carte des incendies (zones rouges) détectés par Modis et Landsat entre 1999 et 2010. Les zones grisées et blanches représentent respectivement les zones forestières et les formations ouvertes (maquis, savanes, fourrés secondaires) dans lesquels les incendies se propagent (occupation du sol modifié de SGT 2008). Les deux encadrés présentent des zooms mettant en avant la propagation des incendies dans les milieux ouverts qui viennent lécher les lisières forestières (tiré de Curt et al. in prep.).*

2.3.4 Succession secondaire

« *I confess, I was surprised to find my theory so perfectly proved in this case* »

H. D. Thoreau
The succession of forest trees (1852)

Après une ouverture du milieu par une perturbation tel qu'un incendie, une suite de changements dans la composition et la structure de la végétation, appelée succession écologique, est observée (Connell and Slatyer 1977; McCook 1994). Lorsque les savanes ne brûlent plus, ce processus de succession conduit au développement de formations forestières secondaires (e.g. Geiger *et al.* 2011; Hennenberg *et al.* 2005b; Russell-Smith *et al.* 2004b; Silva *et al.* 2008; Swaine *et al.* 1992). Différents facteurs limitent synergiquement la mise en place d'une succession secondaire dans les milieux ouverts tels que les savanes (Holl 1999; Zimmerman *et al.* 2000). L'établissement d'arbres 'forestiers' en savanes passe toutefois par deux phases critiques, (i) l'apport de graines, (ii) la croissance et la survie des individus (Figure 2.10):

(i) La disponibilité en graines sur le site, déjà présentes ('banque de graines') ou apportées *via* des processus de dispersion, constitue l'une des principales barrières à l'établissement de nouvelles espèces (e.g. Cubina and Aide 2001; Hooper *et al.* 2005). L'apport de graine par dispersion et un processus complexe qui dépend à la fois de l'importance et de la répartition spatiale des sources de graines mais aussi de leurs modes de dispersion. Bien que l'apport de graine depuis une source vers un site donné dépende principalement de la distance qui les sépare (Clark *et al.* 1999; Muller-Landau *et al.* 2008; Nathan and Muller-Landau 2000), les patrons de dispersions des graines résultant d'agents biologiques tels que les oiseaux sont les plus complexes (McDonnell and Stiles 1983). En effet, ces derniers sont déterminés par le comportement des disperseurs qui est lui-même influencé non seulement par la structure et la composition du paysage (e.g. Herrera and Garcia 2010; Levey *et al.* 2005) mais aussi par l'attractivité du site lui même (e.g. Fink *et al.* 2009; Medellin and Gaona 1999).

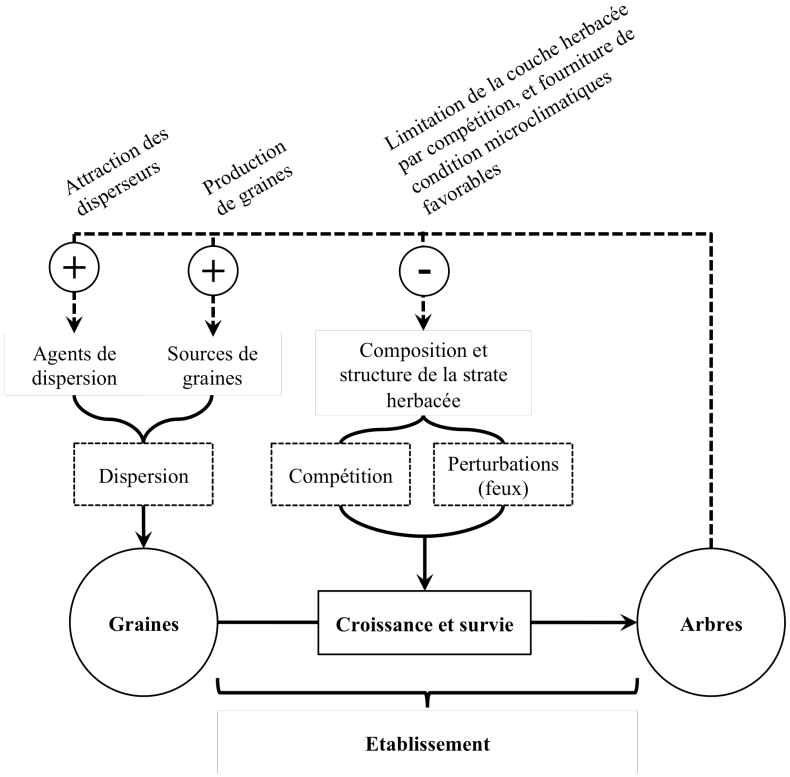


Figure 2.10 *De la graine à l'arbre, barrières à l'établissement d'arbres et rétroactions positives.*

(ii) La croissance et la survie des plantules et des jeunes arbres issues de la germination d'une partie de ces graines sont affectées d'une part par la compétition avec la strate herbacée pour la ressource (lumière, eau et nutriments), et d'autre part, par les perturbations (Bond 2008; Scholes and Archer 1997). Cependant bien que la compétition avec les herbacées puisse limiter l'établissement des arbres (e.g. Davis *et al.* 1999; Williams *et al.* 2005), seuls les incendies semblent pouvoir totalement l'empêcher (Hoffmann *et al.* 2004). En effet, étant donné que les savanes brûlent fréquemment (parfois chaque année) les jeunes individus n'ont que peu de temps pour acquérir les attributs nécessaires pour survivre à un prochain incendie (Gignoux *et al.* 2009). Différentes stratégies de survie peuvent être distinguées (Gignoux *et al.* 1997; Scutz and Bond 2009; Vesk 2006) : (i) investir dans des défenses, via l'écorce et la croissance en hauteur pour résister au passage de l'incendie (Hoffmann *et al.* 2003; Jackson *et al.* 1999), (ii) investir dans des réserves racinaires pour persister, puis rejeter après le passage de l'incendie (Bond and Midgley 2001; Higgins *et al.* 2000).

Cependant le temps nécessaire à une espèce pour atteindre la taille lui permettant de résister au passage du feu (appelé taille d'échappement) est un trait majeur pour qu'une espèce atteigne sa taille mature dans un écosystème soumis aux incendies (Gignoux *et al.* 2009). Ainsi, l'établissement d'arbres forestiers en savane nécessite de forts compromis d'investissement (Figure 2.11) entre croissance des racines et de l'appareil photosynthétique pour augmenter la compétitivité face aux herbacées, et investissement dans les défenses et / ou les réserves racinaires pour survivre aux incendies (Gignoux *et al.* 2009; Scutz and Bond 2009).

Il faut noter que les changements dans la structure et la composition de la strate herbacée due aux espèces invasives peuvent limiter l'installation des arbres en augmentant la compétition (e.g. Denslow *et al.* 2006; Hoffmann and Haridasan 2008) et en modifiant le régime d'incendie (e.g. Brooks *et al.* 2004; Mistry and Berardi 2005). A l'inverse la présence ou l'installation d'arbres en début de succession secondaire entraine une rétroaction positive sur la succession secondaire. En effet, ces arbres par leur ombrage limitent la strate herbacée diminuant ainsi la compétition et possiblement la fréquence d'incendie tout en offrant des conditions microclimatiques plus favorables aux espèces forestières (Hoffmann 1996; 2000). Ils provoquent aussi une rétroaction positive sur l'apport de graines en produisant à leur tour des graines mais aussi en augmentant l'attractivité du site *via* l'effet perchoir (e.g. Guevara *et al.* 1986; Slocum and Horvitz 2000).

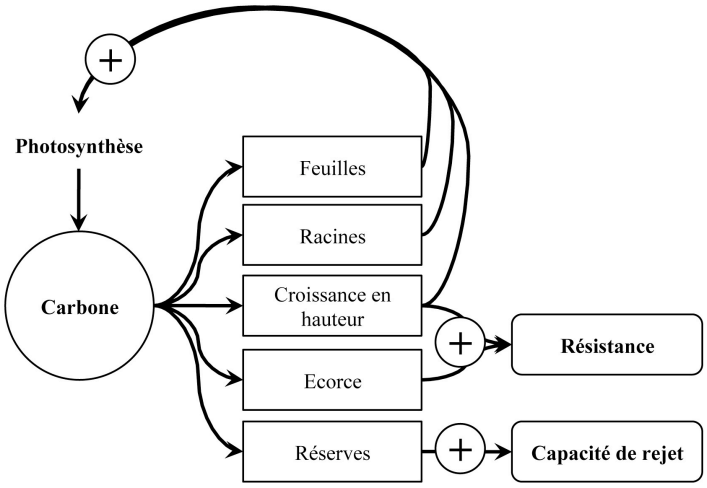


Figure 2.11 *Compromis d'investissement du carbone au cours de l'établissement d'un arbre dans une savane soumise aux incendies.*

2.4 Objectifs et démarche scientifique

En Nouvelle-Calédonie, les incendies sont considérés comme l'une des principales menaces pesant sur les forêts denses humides qui sont les écosystèmes naturels néo-calédoniens les plus riches en termes de biodiversité. Vraisemblablement rongées par les incendies, les forêts denses humides sur substrats volcano-sédimentaires semblent peu à peu être remplacées par des savanes. Cependant, malgré les enjeux biologiques et socio-économiques, les processus mis en jeux lors de cette contraction forestière ou inversement lors de la recolonisation de ces savanes par succession secondaire restent très peu connus. Ainsi l'objectif général de cette thèse est d'ouvrir ce champ de recherche en Nouvelle-Calédonie afin de fournir les connaissances et les outils nécessaires aux gestionnaires pour la conservation et la restauration de ces écosystèmes.

Les principales hypothèses de ce travail de thèse sont que les incendies sont le principal facteur créant et maintenant les savanes, et qu'une diminution de la fréquence des incendies permet une recolonisation forestière.

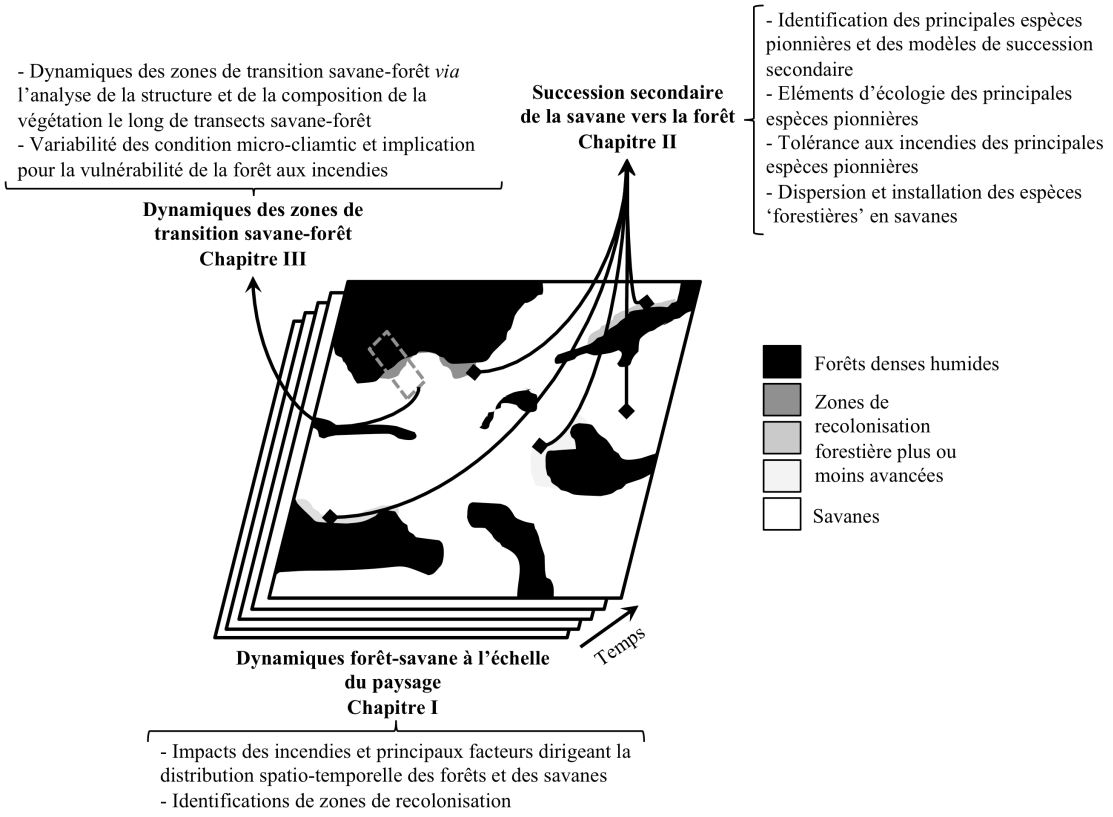


Figure 2.12 *Démarche scientifique et présentation des différents chapitres de cette thèse.*

Chapitre I : Les savanes et les forêts denses humides peuvent être deux états alternatifs stables dont la distribution dépend du régime des incendies. Ces deux états se retrouvent dans un même paysage où ils forment une mosaïque de savanes et de forêts. Le passage d'un état à l'autre dépend de processus spatiaux : la propagation des incendies et la dispersion des graines à la base de la succession secondaire. Dans le premier chapitre de cette thèse nous testons les hypothèses selon lesquelles (i) la distribution spatio-temporelle des savanes et des forêts denses humides dans le paysage montagneux de la Nouvelle-Calédonie dépend de la topographie qui affecte entre autre le comportement et le régime d'incendie et que (ii) la probabilité de passage d'un état à un autre dépend de la structure et de la composition du voisinage.

Ces premiers travaux basés sur l'analyse d'une série diachronique de photographies aériennes (1955-2000) ont permis de préciser l'impact des incendies et d'identifier les facteurs dirigeant la distribution spatio-temporelle des forêts denses humides et des savanes dans les paysages néo-calédoniens. Les facteurs humains à priori pas pris en compte se sont révélés être un facteur explicatif de cette structure paysagère. Ces travaux ont aussi permis d'identifier des zones d'expansion forestière où aller analyser les processus de succession secondaire (Figure 2.12).

Chapitre II : Une modification du régime d'incendies dans les savanes (baisse de leurs fréquences) permet la mise en place de successions secondaires permettant la conversion de savanes en formations forestières secondaires. Le second chapitre de cette thèse analyse une série de processus liés à ces successions secondaires. Dans une première partie, nous faisons l'hypothèse que des différences dans l'écologie (dispersion et tolérance à l'ombrage) des espèces de début de succession peuvent mener à différents modèles de succession secondaire. A partir de relevés floristiques effectués au cours de cette thèse et de données d'herbier, cette partie a permis d'identifier plusieurs modèles de successions à travers différents cortèges d'espèces pionnières, post-pionnières et forestières. Des résultats supplémentaires sur l'analyse de la structure spatiale de ces zones de recolonisation viennent compléter l'analyse de cette première partie du chapitre (Figure 2.12).

Dans une seconde partie, nous testons l'hypothèse selon laquelle la tolérance aux incendies des différentes espèces pionnières identifiées varie, et ce en fonction de leurs

traits de résistance aux incendies (épaisseur de l'écorce et hauteur du houppier) et des modèles de développement de ces traits (relations allométriques). Cette partie a permis d'identifier, à partir de la combinaison de mesures de traits fonctionnels, d'un modèle de comportement des incendies (BEHAVE) et de modèles semi-physiques de dommages causés par le feu, les espèces les plus à même de s'établir facilement dans les savanes. Cette partie est elle aussi complétée par des résultats supplémentaires sur l'analyse plus poussée de la dynamique de l'espèce dominante des savanes néo-calédoniennes (Niaouli, *Melaleuca quinquenervia*) face aux incendies.

Dans une troisième partie, nous testons l'hypothèse selon laquelle l'installation de deux de ces espèces en savanes permet une augmentation de l'apport de graines en savane par effet perchoir. Nous avons mesuré l'apport de graines en savane et sa variabilité spatio-temporelle à partir de pièges à graines installés et relevés bimensuellement sur près d'une année. Cette partie est complétée par des résultats supplémentaires préliminaires sur l'analyse de l'impact d'une espèce invasive (*Lantana camara*) sur l'établissement des arbres en savane.

Chapitre III : Les zones de transition entre savane et forêt dense humide constituent des zones charnières dans la dynamique de ces paysages. Dans le troisième chapitre de cette thèse nous analysons la structure, la composition et les conditions microclimatiques de ces zones de transitions (Figure 2.12). Dans une première partie, nous faisons l'hypothèse que la structure de ces zones de transition peut s'analyser au travers de la mise en évidence de changements abrupts ou graduels dans les assemblages floristiques et que la structure des populations témoigne de leurs dynamiques. Cette partie nous a permis de compléter notre connaissance des successions forestières et d'identifier des espèces témoins des différents stades de la dynamique savane-forêt. Dans une seconde partie, nous testons l'hypothèse selon laquelle la dessiccation de cette zone de transition par effet de bord permet aux incendies se propageant en savane de se propager dans le sous-bois forestier et *in fine* de ronger la forêt.

2.5 Objectives and approaches

In New Caledonia, fires are considered as one of the main threats to rainforests, which are ones of the richest natural ecosystems in terms of biodiversity in New Caledonia. Rainforests on volcano-sedimentary substrates, which are pushed back by bush fire, are gradually replaced by savannas. Indeed, the reccurrence of savanna fires over the last decades have promoted the feeling in local populations that rainforests on volcano-sedimentary substrates may be pushed back by bush fires and gradually replaced by savannas. However, despite the biological and socio-economic stakes such change could induce, forest contraction and expansion and related processes have remained unstudied. Thus, the overall objective of this thesis was to open this field of research in New Caledonia in order to provide knowledge and tools to managers for the conservation and restoration of these likely threatened ecosystems.

The main working assumptions of this thesis are that (i) fires are the main factor creating and maintaining savannas, and (ii) a decrease in fire frequency allows forest recolonization by secondary succession.

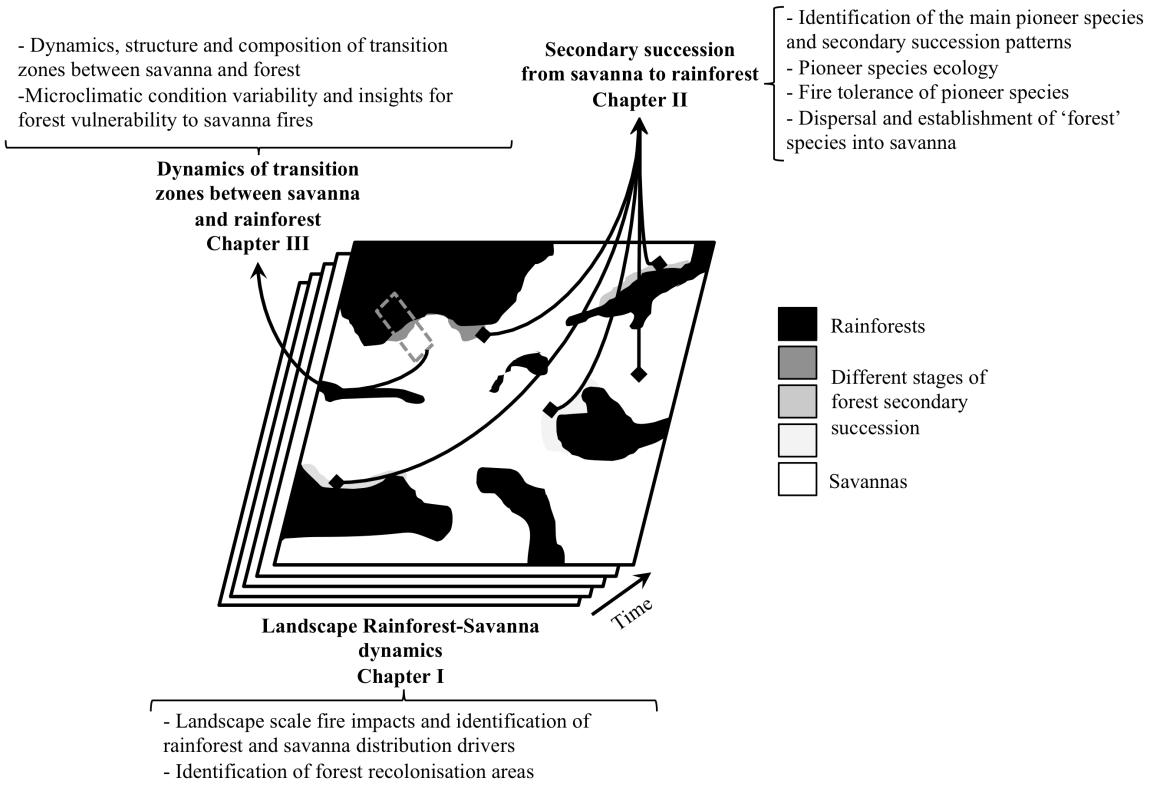


Figure 2.13 *Scientific approaches and overview of the chapters of this thesis*

Chapter I: Savanna and rainforest may be two alternative stable states, which are driven by fire regime. These two states are found in the same landscape where they form a mosaic. The transition from one state to the other depends on spatial processes: the spread of fire and the dispersal of seeds, which is the first barrier to secondary succession. In the first chapter of this thesis we tested the hypotheses that (i) savanna and rainforest patches have changed of the last decades, and that their spatial and temporal distribution in the hilly landscape of New Caledonia depends on topography, which affects several fire behavior and fire regime variables, and (ii) that the probability of transition from one state to the other depends on the structure and composition of the neighbourhood.

This work based on the analysis of a temporal series of aerial photographs (1955-2000) has both located state changes likely due to the impact of fires and identified the factors that drive the spatio-temporal distribution of rain forests and savannas in this New Caledonian landscape. We also found that human factors linked to fire use are important factors that drive the landscape structure. This work has also identified areas where forest has expanded to analyze the process of secondary succession (Figure 2.13).

Chapter II: A change in savanna's fire regime (mainly a decrease in frequency) allows the establishment of secondary succession and the development of secondary forest formations in savanna. The second chapter of this thesis analyzed several processes related to this secondary succession. In the first part, we hypothesized that differences in ecology (seed dispersal and shade tolerance) of early successional species can lead to different patterns of secondary succession. From floristic surveys conducted during this thesis in recent forest patches combined to herbarium data, this section has identified two secondary succession patterns through different floristic assemblages of pioneer, post-pioneer and forest species. Supplementary results on the analysis of the spatial structure of these areas of recolonisation complete the analysis of this first part of the chapter (Figure 2.13).

In the second section, we hypothesized that the fire tolerance of the identified main pioneer species is highly variable according to species-specific traits allowing resisting or avoiding fire effects, in particular difference in investment in bark and

height. In this section, we identified from a combination of functional traits measurements, fire behavior simulation (BEHAVE) and fire-caused damages estimation (using semi-physical models), the species most likely to establish easily into fire prone savannas. This section was completed with supplementary results about the dynamics of the savanna dominant tree species of New Caledonia (Niaouli, *Melaleuca quinquenervia*) in response to fires.

In the third section, we test the hypothesis that the establishment in savannas of two of these pioneer species increases the seed-rain because of the perch effect. We used seed-traps to measure the seed-rain in savanna and its spatio-temporal variability during nearly one year. This section was completed by supplementary results about the analysis of the impact of an invasive species (*Lantana camara*) on the establishment of trees in savanna.

Chapter III: The transition between savanna and rainforest is a critical zone for the dynamics of these landscapes. In the third chapter of this thesis we analyzed the structure, composition and microclimatic conditions of these transition zones (Figure 2.13). In the first section, we tested the hypothesis that the structure of the savanna-forest transition zone with sharp (boundaries) and / or gradual transitions (ecotones) in floristic assemblages and population structures may point out its spatio-temporal dynamics. This section allowed us to complete our knowledge about forest succession and to identify indicator species for the different successional stages of savanna-forest dynamics. In the second section, we tested the hypothesis that desiccation of this transition zone by edge effect allows savanna fire to spread into the forest understory and finally to push back the forest edge.

Chapitre I

3 Rainforest and savanna landscape dynamics in New Caledonia: Towards a mosaic of stable rainforest and savanna states?

This section is submitted (since June 23rd 2011) to *Austral Ecology* as the following research paper :

Ibanez, T., Borgniet, L., Mangeas, M., Gaucherel, C., Géraux, H., and Hély, C., (submitted). Rainforest and Savanna Landscape Dynamics in New Caledonia: Towards a mosaic of stable Rainforest and Savanna states?, submitted to *Austral Ecology*.

3.1 Résumé

Les forêts et les savanes peuvent être deux états stables alternatifs très contrastés qui peuvent passer d'un état à l'autre lors de perturbations. Ainsi, comme dans le point chaud de biodiversité néo-calédonien, les forêts soumises aux changements anthropiques environnementaux peuvent être convertis en savanes conduisant à d'importantes pertes écologiques et économiques. A l'échelle du paysage, les systèmes soumis à de tels changements sont caractérisés par des frontières abruptes entre forêts et savanes et par la formation de mosaïques. Comprendre la structure et les dynamiques de tels systèmes est un challenge pour les écologues et enjeu majeur pour la gestion des paysages et la conservation de la biodiversité. En utilisant une série de photographies aériennes (de 1955 à 2000) et un indice de qualité de l'habitat, nous testons l'hypothèse selon laquelle la topographie et les processus spatiaux vraisemblablement liés à la propagation des feux et la dispersion des graines sont les principaux déterminants de la distribution spatial des forêts et des savanes dans le paysage. Sur les 24-km^2 du paysage étudié, la couverture forestière a diminuée de 24 pourcent entre 1976 et 2000. Cette perte, est principalement due à la contraction des forêts exposées à l'ouest qui représente près de 90 pourcent de la perte de couverture forestière totale, alors que les forêts exposées à l'est semblent d'hors et déjà limitées et confinées à des refuges. L'indice de qualité de l'habitat calculé à partir de variables topographiques en utilisant des modèles additifs généralisés a été un prédicateur performant des probabilités de présence, d'expansion ou de contraction de la forêt. Cependant, nous montrons aussi que des processus spatiaux tels que la propagation d'incendie ou la dispersion des graines limite respectivement la contraction et l'expansion de la forêt. Nos résultats suggèrent que les forêts exposées à l'ouest vont être progressivement détruites par les incendies jusqu'à ce qu'elles soient aussi confinées aux refuges.

Mots clés: Feux, Modèles additifs généralisés, indice de qualité de l'habitat, variables topographiques, forêt tropical, refuges.

3.2 Abstract

Stable forested environments can be converted to savanna in response to changes in environmental disturbances. New Caledonia is a biodiversity hotspot; significant ecological and economic resources would be lost if forests were turned into savanna by anthropogenic environmental changes. On the landscape scale, systems that have undergone shifts of this kind are characterized by sharp forest-savanna boundaries and mosaic-like distributions of savanna and forest. Understanding the locations and the dynamics of such boundaries is a challenge for ecologists and is critical for landscape management and biodiversity conservation. Using a time series of aerial photographs (1955-2000) and a forest habitat suitability map, we tested the hypothesis that topography and spatial processes, especially those relating to fire spread and seed dispersal, are the main determinants of the spatial distribution of rainforest and savanna in a New Caledonian landscape covering 24 km^2. Within the studied landscape, the overall forest coverage decreased by 24 % between 1976 and 2000. This was primarily due to the contraction of forests on west-facing slopes, which accounted for *ca* 90 percent of the total loss. Conversely, the east-facing forests seemed to have contracted extensively prior to the studied period, and were confined to refuges. A habitat suitability index calculated from the landscape's topographical features using generalized additive models accurately predicted both the presence of forests and the probability of forest expansion / contraction. We also provide evidence that spatial processes such as fire spread and seed dispersal limit the expansion and contraction of forests. Our results suggest that rainforests on west-facing slopes in New Caledonia will be progressively destroyed by fire until they are restricted to refuges along thalwegs and creeks, as appears to have already happened for their east-facing counterparts.

Keywords: fire**,** generalised additive model (GAM); habitat suitability index (HSI); topographical landscapes features; refuges.

3.3 Introduction

Habitat loss is one of the main causes of the current biodiversity crisis (Brooks *et al.* 2002; Wright and Muller-Landau 2006a) and the global rate of forest habitat destruction remains alarmingly high (FAO 2010). In the tropics, forested landscapes that are subjected to anthropogenic and environmental changes can be converted to savannas, resulting in large losses of biological, ecological and economic resources (Folke *et al.* 2004; Scheffer and Carpenter 2003). Indeed, in certain landscapes, forest and savanna may represent two alternative stable states (ASS) that can be interconverted in response to specific environmental perturbations (Bond 2008; Hirota *et al.* 2011; Scheffer and Carpenter 2003). Systems supporting ASS are characterized by sharp boundaries between vegetation types and the presence of landscape-scale mosaics (Warman and Moles 2009). Understanding the factors that control the locations and dynamics of the boundaries in systems such as forest-savanna mosaics is a challenge for ecologists and is critical for landscape management and biodiversity conservation (see Bond 2008; Warman and Moles 2009).

In contrast to forests, savannas are characterized by a continuous grass layer with discontinuous tree cover (Scholes and Archer 1997). Ecologists have long been interested in the coexistence of these two contrasting plant types, i.e. trees and grasses (*e.g.* Gardner 2006; Sankaran *et al.* 2004; Scholes and Archer 1997). In a recent review, Bond (2008) outlined the key factors that restrict the growth and spread of trees and thereby allow trees and grasses to coexist (and thus permit the existence of savannas). These include factors that exert bottom-up control, such as the availability of water and nutrients (resources), and those that effect top-down control, including disturbances such as fire and grazing (consumers, see Bond and Keeley 2005). Broad scale studies on African savannas have demonstrated that resource availability, and especially that of water, imposes a theoretical upper limit on the extent of the tree cover that can be established within a given environment, and that disturbances such as fires maintain the actual tree cover at some level below this maximum (Bucini and Hanan 2007; Sankaran *et al.* 2005; Staver *et al.* 2011a). Recently, on a global scale Staver *et al.* (2011b) highlighted the critical role of fire in the differentiation of high and low tree cover (*i.e.*

forest and savanna, respectively) in areas receiving intermediate rainfall (from 1000 mm to 2000 mm per year).

In the New Caledonian biodiversity hotspot (Mittermeier *et al.* 2004; Myers 1988) more than the half of the original vegetation (mainly forest) has already disappeared (Jaffré *et al.* 1998). Palaeoecological records suggest that following the arrival of humans (*i.e.* the Melanesians around 3000 years BP and Europeans in the mid-1800s), the fire regime in the region changed, with the frequency of fires increasing significantly, and that this coincided with the sudden appearance of savannas in the New Caledonian landscape (Hope and Pask 1998; McCoy *et al.* 1999; Stevenson 2004). Sharp transitions of this kind whereby forests are converted to savannas in very short periods of time are consistent with the ASS hypothesis (Warman and Moles 2009).

Today, the only bush fires that occur in the region are man-made, and the savannas, which are maintained by those fires and by grazing (Jaffré and Veillon 1994), cover almost 30 percent of the main island, having effectively replaced both dry forest (see Bouchet *et al.* 1995; Gillespie and Jaffré 2003) and rainforest (Jaffré and Veillon 1994). Consequently, the rainforest is rare and fragmented at low and intermediate altitudes; extensive contiguous areas of rainforest are found only at high altitudes or in inaccessible areas (Jaffré *et al.* 1998; Jaffré and Veillon 1994). Within the island's central mountain chain, there are no farms and no logging operations are conducted; as such, grazing and logging pressures are insignificant. As such, the largest areas of native rainforest on the island are found in this region, which is where the study reported herein was conducted. Given the absence of farming and logging, it was assumed that inland bush fires are the main disturbance that has created and maintained the savannas of the region's rainforest-savanna mosaic. Within this region, the behaviour of variables that affect fire behaviour and fire size (*e.g.* relative humidity, direction and nature of winds, and fuel moisture) are primarily dependent on the local topography (Whelan 1995), which also has a profound influence on the distribution of rainforest and savanna.

In this paper, we present an analysis of the spatial distribution of rainforest and savanna and their temporal dynamics in a hilly New Caledonian landscape under anthropogenic fire pressure. We used a time series of aerial photographs (from 1955 to 2000), GIS and statistical modelling (Generalised Additive Models) to describe and

analyze the spatiotemporal variability of the coverage of rainforest and savanna, and tested the hypothesis that topography and spatial processes (which are presumably related to fire spread and seed dispersal) are the main determinants of the spatial distribution of rainforest and savanna in the landscape. Particular emphasis was placed on understanding (1) how topography structures the distribution of rainforest in the landscape, and (2) how the spatial distribution rainforest and savanna drive forest expansion-contraction. To address issue (1), we constructed an index of rainforest habitat suitability that could be regarded as an "*index of topographic fire protection*" (Table 3.1) using the terminology of Brook & Bowman (2006). Finally, we discuss how other environmental and anthropogenic changes (Lewis 2006), such as the introduction of invasive species, socio-economic change, and climate change might influence rainforest coverage through their impact on fire regimes and succession processes.

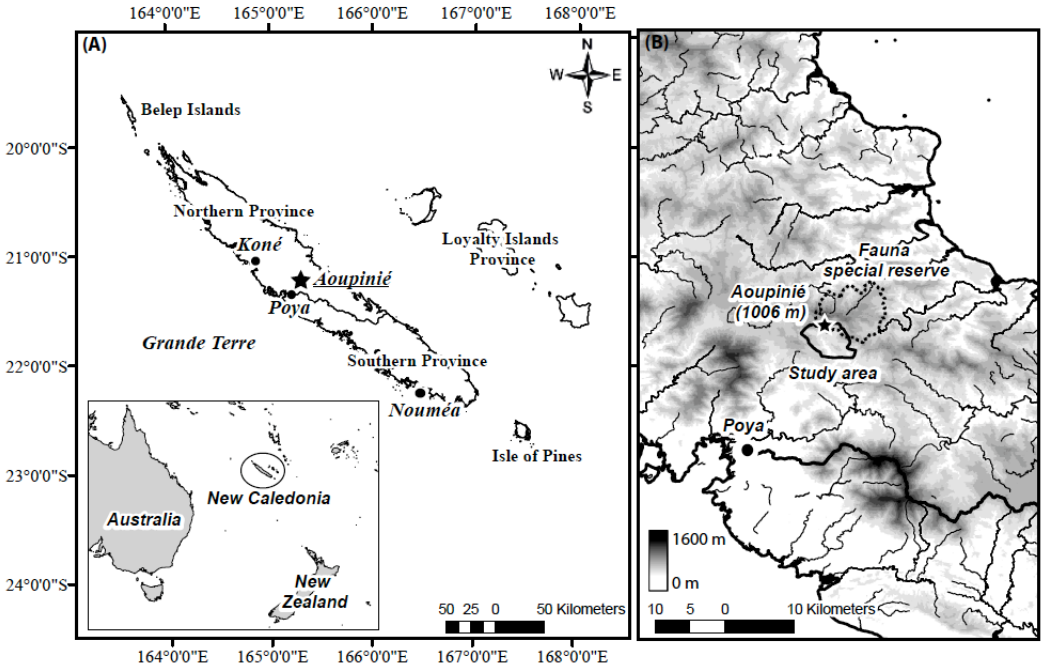


Figure 3.1 *Location of the study area. (A) The location of New Caledonia in Oceania, and the location of the study site (Aoupinié, black star) in New Caledonia. (B) Location of the 24-km^2 study area (thick dark line) next to the Aoupinié special fauna reserve (dotted thick dark line) in the middle of the New Caledonian Grande Terre with elevation (grey scales) and primary hydric network. The elevation of the study area ranged from 90 and 650 m asl, with a maximum slope of 60°.*

Table 3.1 *Topographical variables used to compute the rainforest habitat suitability index (HSI) on the basis of their known impact on fire ecology.*

Variable		Influence on fire ecology
Aspect (°)	As.	*Locations whose aspect leaves them exposed to the prevailing wind have more frequent and more intense fires.* Rationale: High exposure to prevailing winds increases fire intensity and reduces humidity and fuel moisture.
Elevation (m asl.)	El.	*The frequency and intensity of fires will be greater at lower elevations.* Rationale: At low elevations, the humidity and fuel moisture should be lower, and the ignition pressure should be higher as a result of proximity to ignition sources (fields, roads…).
Slope (°)	Sl.	*The frequency and intensity of fires will be greater on steeper slopes.* Rationale: Fires on steeper slopes should spread more easily and be more intense due to higher combustion completeness.
Curvature (indices)	Cu.	*The frequency and intensity of fires will be greater around convex landscape features (i.e. ridges).* Rationale: Humidity and fuel moisture should be lower, and wind exposure should be higher on convex features.
Distance from river (m)	Dr.	*The frequency and intensity of fires will be greater in regions that are far from watercourses.* Rationale: Humidity and fuel moisture should decline as the distance from the nearest watercourse increases.

3.4 Materials and methods

3.4.1 Study area

The New Caledonian archipelago is a French overseas territory located in the southwest Pacific (20°-23°S and 164°-167°E, Figure 3.1.A), in the inter-tropical zone, close to the Tropic of Capricorn. The climate is tropical oceanic with a cool (from June to September) and a hot (from October to May) season, both of which overlap with a characteristic dry season that runs from August to November. The dry season is also the bush fire season, and is characterised by low rainfall, rising temperatures, and near-constant easterly *alizé* trade winds. The variability of the New Caledonian climate is primarily governed by the *El Niño* Southern Oscillation (ENSO) phenomenon (Ropelewski and Halpert 1987), *i.e.* during *El Niño* phases the rainfall decreases (to less than 50 % of its usual value), whereas during *La Niña* phases the opposite trend is observed (Delcroix and Lenormand 1997).

Despite its small size (ca 19,000 km^2), New Caledonia has a particularly rich and unique population of flora (it is home to approximately *ca* 3500 *taxa* of vascular plants, with close to 75 % endemicity, Jaffré *et al.* 2001). This exceptional biodiversity is attributable to its unusually complex geological history (Grandcolas *et al.* 2008) and is supported by a mosaic of ecosystems linked to different substrates, rainfall regimes and human activities (Jaffré *et al.* 1998). Rainforests with annual rainfall levels ranging from 1300 to more than 3500 mm per year cover approximately 3800 km^2 of New Caledonia (Jaffré *et al.* 2009).

The study area is located in the western part of the central mountain chain and close to the border of the two provinces of the main island (*Grande Terre*), *i.e.* the Northern and Southern provinces (Figure 3.1.B). Specifically, the study area is on the western side of the *Aoupinié* mountain (1006 m, 21°11'S and 165°15'E), which - shelters one of the largest rainforest areas on acidic soils (volcano-sedimentary substrate) in the archipelago, including a special fauna reserve covering 5400 ha. The 24-km^2 study area is located in the foothills of *Aoupinié* (*ca* 100-650 m asl); it is crossed by the *Poya* river and includes a portion of the territory of one of the largest tribes of New Caledonia (the *Gohapin*, which has *ca* 700 members). The mean annual

precipitation at the site ranges from 1500 to 3000 mm (METEO-France 2007). The landscape mosaic consists of wooded savannas dominated by Niaouli (*Melaleuca quinquenervia* S.T.Blake) with patches of rainforest.

The fire regime within the study area is poorly known. During a recent study of the area conducted over six months in 2009 (May, June and November) and 2010 (March, October and November), 96 fires were recorded, affecting areas of 0.1 to 20 ha (1.5 ± 1 ha on average). However, these years were abnormally humid (*la Niña* episode) and are not representative of the extent of the fire pressure. During abnormally drought years (*el Niño* episodes) fires are larger, more numerous and more intense, and all or almost all the savanna is burned (see Barbero *et al.* in press. for more presision on fire regime at the New Caledonian scale).

3.4.2 Mapping rainforest change

Maps of rainforest change from 1955 to 2000 were produced by analysing forest / non-forest maps extracted from a chronological series of aerial photos. Almost all of the non-forest areas consisted of savanna, but other cover types were also identified, including cultivated land (used for subsistence farming) and thickets. The historical aerial photos of the study site (taken in the years 1955, 1976, 1985, 1997 and 2000) were scanned and re-sampled to achieve a common 1-m cell resolution. These aerial photos comprise both black and white photos (those taken in the years 1955 [1 : 25 000], 1976 [1 : 25 000], 1985 [1 : 40 000]) and colour photos (those taken in 1997 [1 : 20 000] and 2000 [1 : 20 000]). Image treatment was performed using the ERDAS Imagine 9.1 software.

All photos were geo-referenced and ortho-rectified using a 10-m digital elevation model (DEM). Since the 1997 photos were of the highest quality and covered the greatest area of land, they were the first to be geo-referenced, ortho-rectified and joined. All other photos were then geo-referenced using the 1997 photo mosaic as a reference. The horizontal root mean square errors (RMSE) were 5.2 m for the 1997 mosaic and less than 5 m in all other cases; the average RMSE was 3.3 m.

Supervised classification was used to assign each image cell as a forest or non-forest cell (coded as 1 or 0, respectively). The validity of the classification method was

assessed by using it to classify 386 randomly selected points and comparing those classifications to those made by an expert; more than 80 percent of the points proved to be well-classified. The spatial resolution of the classified images was degraded from 1 to 10 m in order to reach the DEM resolution deemed most suitable for studying rainforest expansion and contraction processes. The increase in scale from 1 to 10-m^2 reduced the amount of noise introduced during classification based on texture analysis at 1-m^2 (intra-crown heterogeneity) and strengthened the delineation of the boundaries between forested and non-forested regions.

Maps of rain forest changes from 1955 to 2000 were obtained by computing image-to-image differences. Two kinds of maps were created (1) forest expansion maps, in which cells that had changed from non-forest to forest were coded as 1 and cells that had done otherwise were coded as 0, and (2) forest contraction maps, in which cells that had changed from forest to non-forest were coded as 1 and the others as 0. All manipulations of data and statistical procedures were conducted using the R 2.9.2 environment (R Development Core Team 2009).

3.4.3 Forest coverage variation

We explored the temporal variation of the forest coverage (in terms of absolute extent and as a percentage of the total forested area) from 1955 to 2000 and the associated rates of change. Since we assumed that exposure to the dominant wind (i.e. the easterly trade wind) was likely to play a major role in determining both the absolute forest coverage and the variation in its rate of change, we obtained quantitative data on this variable for both east- (*i.e.* < 180°) and west- (*i.e.* > 180°) facing areas. We then analysed the spatiotemporal variation in forest coverage by studying the mean forest coverage (FC) and its standard deviation (SD) in 1955, 1976, 1985, 1997, and 2000 in relation to the features of the studied landscapes (*i.e.* elevation, aspect, slope, curvature and distance to the nearest river distance), as determined by inspection of the 10-m DEM.

3.4.4 Forest habitat suitability map

A niche-based model was constructed to analyse our forest presence-absence data; models of this kind are widely used to model species distributions and to create habitat suitability (HS) maps (Guisan and Thuiller 2005). We used a GIS-based model to establish a HS Index (HSI) that describes the suitability of an area for the establishment and persistence of forests in the hilly landscape of New Caledonia. The value of the HSI for a given area is determined by the likelihood of forests being present in areas with similar characteristics, and ranges from 0 for wholly unsuitable areas to 1 for the most suitable areas. The dependent variable in the model is the presence or absence of a forest in the area in question (the variable takes a value of 1 when forests are expected to be present and 0 otherwise), and the features of the landscape (Table 3.1) are the predictors. In order to take the temporal information into account, a HSI model was built for each of the 5 years for which data were available; the final HSI map was computed by averaging the 5 single-year HSI maps.

The HSI was computed using generalised additive models, or GAMs (Hastie and Tibshirani 1986); the GAM is a nonparametric generalization of the generalized linear model, GLM (McCullagh and Nelder 1989), in which the linear predictor is specified as a sum of smooth functions. GAMs are data-driven models (Guisan et al. 2002) that focus on exploring data non-parametrically, whereas parametric models such as GLMs rely on estimation and inference to determine the values taken by the parameters. We used the R function *gam* from the library *mgcv* (Wood 2001) to fit GAMs with a binomial probability distribution and a logit-link function. We considered all landscape features independently, focusing exclusively on the two-way interactions between the different variables. More complex interactions were not considered to facilitate ecological interpretation.

A split sample approach was used to calibrate and validate the GAMs (Guisan and Zimmermann 2000). Thus, the study area was divided into 16 strips; the GAMs were calibrated on a randomly selected subsample of half of these and validated on the other half in order to assess the extrapolation capacities of the different models. The strips were defined so as to ensure that the widest possible ranges of the various predictors were considered during model calibration and validation. The models'

goodness of fit was assessed using the D^2 statistic (Guisan and Zimmermann 2000); the accuracy of the models' predictions relative to the observed results was measured using the Kappa (K) index (Cohen 1960). We analysed the spatial structure of the GAMs' residuals and measured their spatial-autocorrelation with Moran's *I* coefficient (Moran 1950) using the R package *spdep* developed by Bivand *et al.* (2009).

3.4.5 Factors that limit forest expansion and contraction

We tested the hypothesis that forest expansion and contraction follows the HSI map, *i.e.* that the probability of a forest to non-forest (F to NF) transition correlates positively with the HSI and that of a non-forest to forest (NF to F) transition correlates negatively with the HSI. The rainforest-savanna dynamics were not monotonous over the entirety of the study period (*i.e.* 1955-2000). We therefore focused on their dynamics between 1976 and 2000, during which period the forest cover decreased continuously (see Appendix I). Moreover, since forest contraction / expansion were assumed to be due to spatial ecological processes such as fire spread (seed dispersal), we explored the relationships between F to NF (and NF to F) transition probabilities and two spatial predictors: (1) the Euclidean distance between each forest cell and the closest non-forest cell on the 1976 map (for NF to F transitions, the predictor used was the distance between the non-forest cell and the closest forest cell); and (2) a neighbourhood index describing the number of non-forest cells surrounding each forest cell on the 1976 map and their proximity to the cell in question (for NF to F transitions, the predictor used was the number and proximity of forest cells around each non-forest cell). Since more than 90 percent of the transitions observed between 1976 and 2000 affected cells within 50 m of a cell of the opposite type (i.e. forest cells within 50 m of a non-forest cell or vice-versa; data not shown), we considered only cells within a 50 x 50-m window of the target cell. For F to NF transitions, a neighbourhood index was calculated for each forest cell by computing a weighted sum of the number of non-forest cells within the 50 x 50m window surrounding the target cell, with the weighting of the non-forest cells decreasing exponentially with their Euclidean distance from the target cell. A similar procedure was adopted for NF to F transitions, involving summing the number of weighted forest cells surrounding non-forest ones.

3.5 Results

3.5.1 Forest coverage between 1955 and 2000

Over the 45 year period studied, the proportion of cells that changed from forest to non-forest or vice-versa ranged from 1.3 percent per year (1955-1976) to 7.4 per year (1997-2000) and was *ca* 25 percent higher in west facing areas than in their east-facing counterparts (Table 3.2). Forest coverage expanded between 1955-1976 (21 years) and then contracted between 1976-2000 (24 years), with the contraction primarily affecting west-facing areas. However, the apparent expansion in forest coverage between 1955-1976 was identified on the basis of only two sets of photographs (one for 1955 and one for 1976) and the 1955 photos were poor quality black and white photos with shaded areas. We therefore chose to focus on the contraction in forest coverage between 1976 and 2000 (see Appendix), as four sets of high quality photos were available for this stretch of time, enabling it to be subdivided into three consecutive periods (1976-1985, 1985-1997 and 1997-2000).

The forest coverage across the landscape as a whole declined by *ca* 24 % between 1976 (maximum coverage 1385.4 ha) and 2000 (1054.1 ha). However, different dynamics were observed in east-facing and west-facing forests: the forest coverage in east-facing regions declined by 8 % (from 496.6 to 457.4 ha), whereas that in west-facing regions fell by almost 33 percent (from 888.7 to 596.7 ha), accounting for approximately 90 % of the total reduction in forest coverage. Moreover, the rate at which western forests were converted to savanna increased after 1976 and was 3 times faster between 1997 and 2000 than it had been between 1976 and 1985 (-3.0 % per year in 1997-2000, versus 1.1 % per year in 1976-1985).

3.5.2 The influence of landscape features on forest coverage

Mean forest cover (FC) correlated strongly with the five landscape variables considered
(

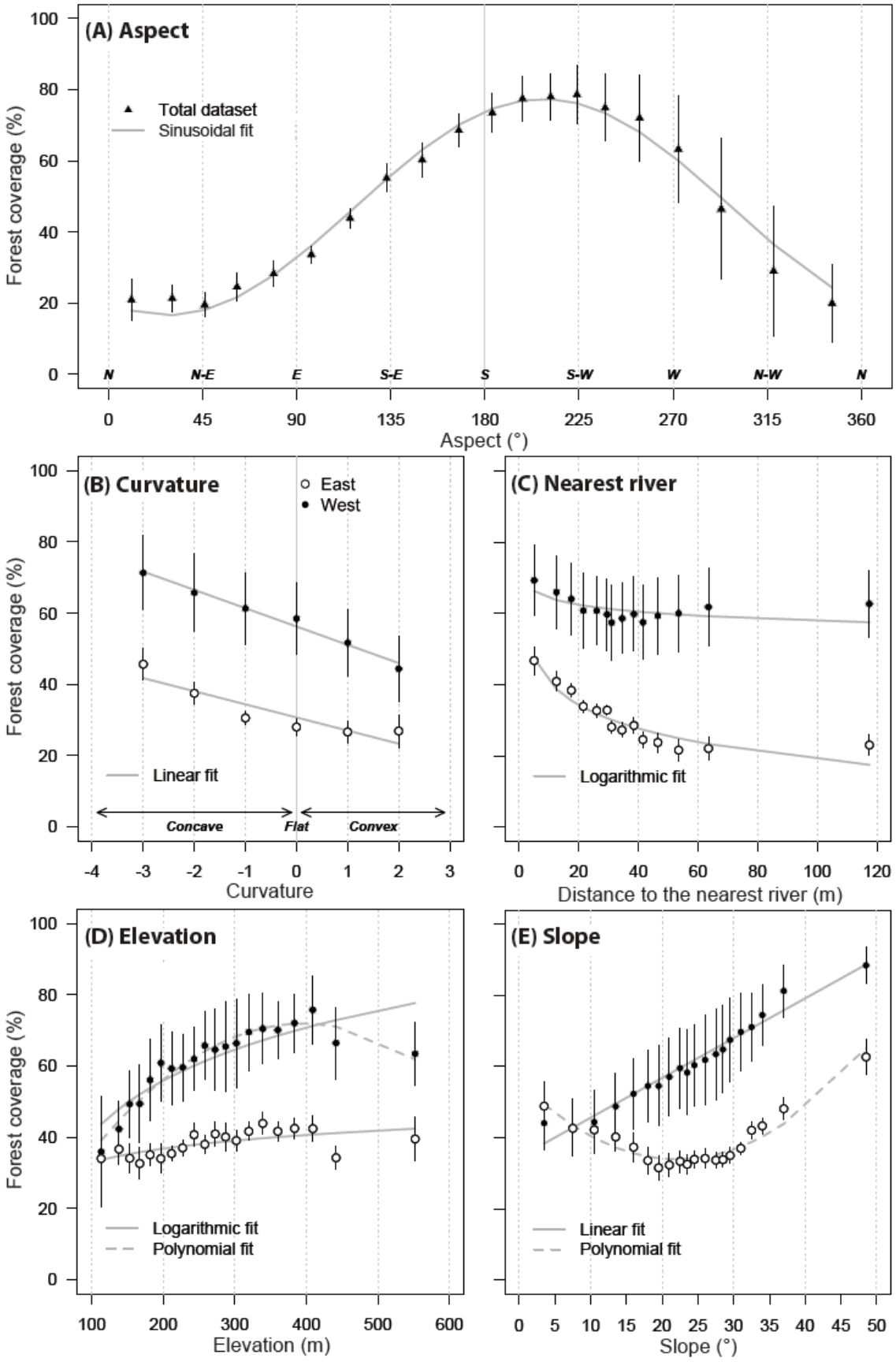
Figure 3.2). As expected, the variable with the strongest FC response was the aspect (As) (

Figure 3.2.A.). This response followed a sinusoidal periodic function (R^2 = 0.98, p-value < 0.05), with the coverage being lowest for areas facing northeast (*ca* 20 %) and highest for areas facing south-west (*ca* 80 %). Furthermore, the average standard deviation in forest coverage over time for west facing areas was twice as great as that for east-facing ones (11.2 ± 5.1 % and 3.9 ± 1.0 %, respectively). This distinct difference in the magnitude and intensity of the responses for eastern and western faces was observed for all of the landscape features examined (Figure 3.2). Eastern forests were preferentially located in concave locations (Figure 3.2.B) and along rivers (less than *ca* 50 m wide, Figure 3.2.C), both of which are characteristic of thalwegs (*i.e.* the line defining the lowest points along the length of a river bed or valley); their coverage was only slightly affected by elevation (*ca* 38 ± 3.5 % from 100 m to 600 m asl, Figure 3.2.D) and to a somewhat greater extent by the steepness of the slope (with the coverage being lowest on slopes of 20 to 30°, Figure 3.2.E). Western forests exhibit similar preferences for thalweg-like conditions (Figure 3.2.B-C), but in contrast to eastern forests, their coverage increased strongly with elevation (Figure 3.2.D) and slope (Figure 3.2.E), doubling on going from the lower to the upper ends of the studied ranges in both cases.

Table 3.2 *Total forest cover for each year examined and changes in forest cover from the previous studied year as a percentage of the total forest cover, for the study site as a whole and for east- and west-facing slopes separately.*

Year	Areas	Forest cover ha (%)	Absolute proportion of change† in % (in % of the area / yr)	Relative forest coverage change† in % (in % / yr)
1955	West-facing areas	716.6 (61.2)	-	-
	East-facing areas	475.2 (38.5)	-	-
	Total	1191.8 (49.5)	-	-
1976	West-facing areas	888.7 (75.9)	28.5 (1.4)	+24.0 (+1.1)
	East-facing areas	496.6 (40.1)	24.7 (1.2)	+4.5 (+0.2)
	Total	1385.4 (57.5)	26.5 (1.3)	+16.2 (+0.8)
1985	West-facing areas	831.0 (70.9)	24.4 (2.7)	-6.5 (-0.7)
	East-facing areas	423.4 (34.2)	23.3 (2.6)	-14.7 (-1.6)
	Total	1254.4 (52.1)	23.8 (2.6)	-9.5 (-1.1)
1997	West-facing areas	713.8 (60.9)	28.8 (2.4)	-14.1 (-1.2)
	East-facing areas	445.8 (36.0)	19.1 (1.6)	+5.3 (+0.4)
	Total	1159.7 (48.1)	23.8 (2.0)	-7.5 (-0.6)
2000	West-facing areas	596.7 (50.9)	25.0 (8.3)	-16.4 (-5.5)
	East-facing areas	457.4 (36.9)	19.7 (6.6)	+2.6 (+0.9)
	Total	1054.1 (43.8)	22.3 (7.4)	-9.1 (-3.0)

Figure 3.2 (next page) *Relationship between forest coverage and topographical landscape features. Points represent the 5-year mean forest cover for quantiles of the explored landscape features (excepted for curvature, which is an index). The relationships for east- and west-facing areas are represented by hollow and filled markers, respectively. The bars denote one standard deviation of the 5 year mean forest coverage; the gray lines (full and dotted lines) indicate the fit of the model to the mean. All presented model fits are significant (p-value < 0.05).*


(A) Aspect
Total dataset
Sinusoidal fit
Forest coverage (%)
N
N-E
E
S-E
S
S-W
W
N-W
N
Aspect (°)
(B) Curvature
East
West
Linear fit
Concave
Flat
Convex
Curvature
(C) Nearest river
Logarithmic fit
Distance to the nearest river (m)
(D) Elevation
Logarithmic fit
Polynomial fit
Elevation (m)
(E) Slope
Linear fit
Polynomial fit
Slope (°)

3.5.3 Forest habitat suitability

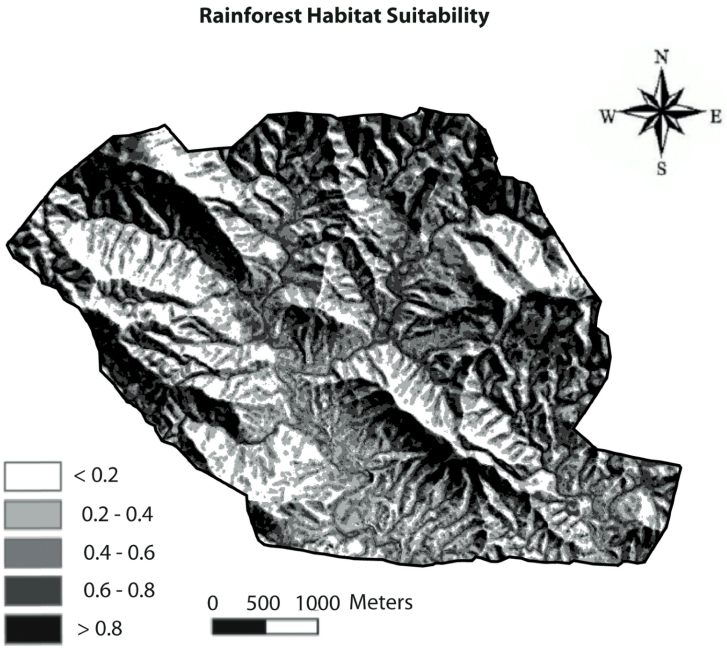


Figure 3.3 *Habitat suitability index (HSI) map for forests, with 5 suitability classes ranging from low suitability (0.0 – 0.2) to high suitability (0.8 – 1.0).*

The HSI model allowed us to efficiently account for both the combined effects of the five landscape features on forest distribution and the consequences of landscape dynamics over the 45-yr period. The global overview of the data provided by the HSI map (Figure 3.3) clearly indicated the high overall suitability of west-facing areas (with the exception of foothill ridges) and the low suitability of east-facing areas (with the exception of the areas along thalwegs). All of the HSI predictors were highly significant (p-value < 0.01), especially the first-order interaction terms (not shown) mainly due to the extensive calibration data-subset used (*i.e.* more than 140,000 cells). Despite the fact that the quality of the fit (D^2) was relatively low (mean 0.42 ± 0.05), the HSI model showed both a good accuracy and extrapolation capacity, as demonstrated using the validation dataset. Indeed, using a HSI threshold of 0.5, the Kappa index indicated moderate to substantial agreement between the predictions of the HSI model and observations, for both the calibration ($K_{0.5}$ = 0.71 ± 0.01) and the validation datasets ($K_{0.5}$ = 0.76 ± 0.02).

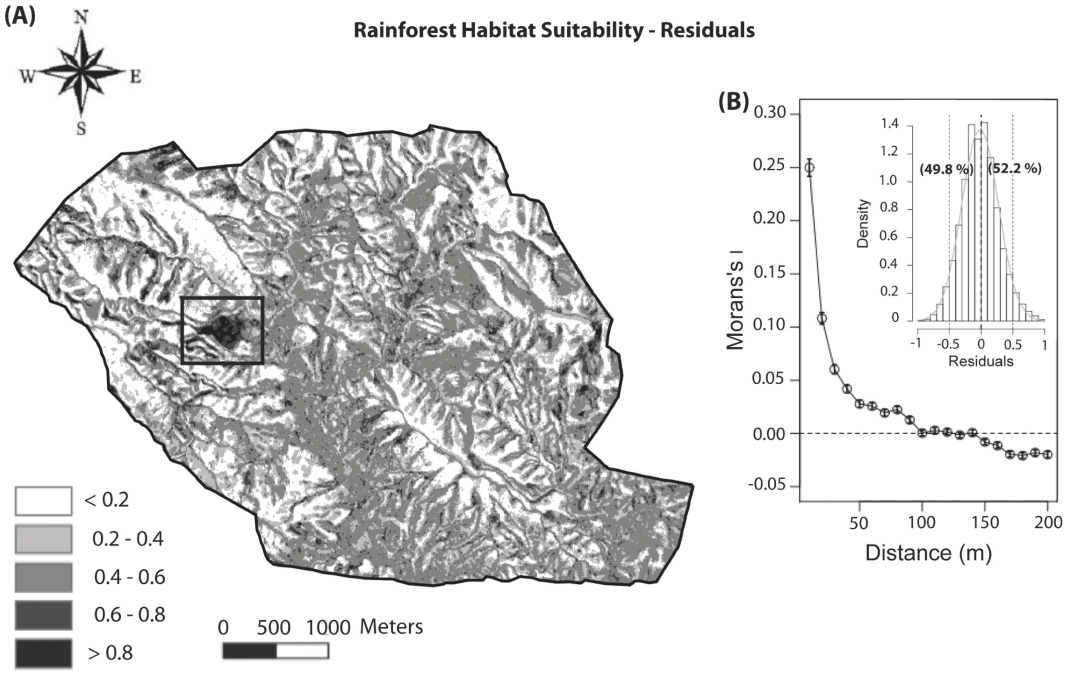


Figure 3.4 *HSI model residuals. (A) Map showing the spatial structure of the residuals (i.e. | observed coverage – HS |), divided into 5 classes ranging from low residuals (0.0 – 0.2, i.e. very good agreement between forest coverage expected on the basis of the HSI and the observed coverage) to high (0.8 – 1.0, i.e. very bad agreement between HS and the observed coverage). The square box highlights a large area with high residuals corresponding to a large patch of forest in an area with a very low HSI. (B) Spatial autocorrelation of residuals, described using Moran's I calculated on a randomly selected data-subset (n = 5000). Distance refers to the inter-cell distance in meters; the error bars indicate the 95 percent confident interval, calculated by randomisation.*

The good performance of the HSI model was confirmed by analysis of its residuals, which were normally distributed, although there was a small amount of spatial auto-correlation for distances of up to 80 m (Figure 3.4.B). This residual spatial structure suggested that there is at least one significant variable that was not included in our HSI model. There map of residuals contains one area (Figure 3.4.A; the area is highlighted in a square box) with unusually high residuals in which there is a large patch of forest in an area with a low HSI value; this apparent anomaly can be explained by considering specific social factors (see the discussion section for more details).

3.5.4 Drivers of forest expansion and contraction

The calculated HSI was a highly significant linear predictor of forest expansion and contraction between 1976 and 2000; high HSI values correlated positively with expansion and negatively with contraction (p-value < 0.05 and $R^2 = 0.94$ in both cases). The probability of observing a transition within a cell decreased exponentially with its distance from the nearest forest edge (Figure 3.6.A-B); this decrease was primarily attributable to the topographical properties (HSI classes) of the cells within 30-m of the edge and to the distance further. In terms of the neighbourhood index, the probability that a non-forest cell would undergo a transition was found to increase with the number of nearby forest cells and their proximity; similarly, the probability of transition for forest cells increased with the number and proximity of non-forest cells. These increases were linear for non-forest to forest transitions and logarithmic for forest to non-forest transitions (Figure 3.6.C-D, respectively); the HSI had only an additive effect on these increases.

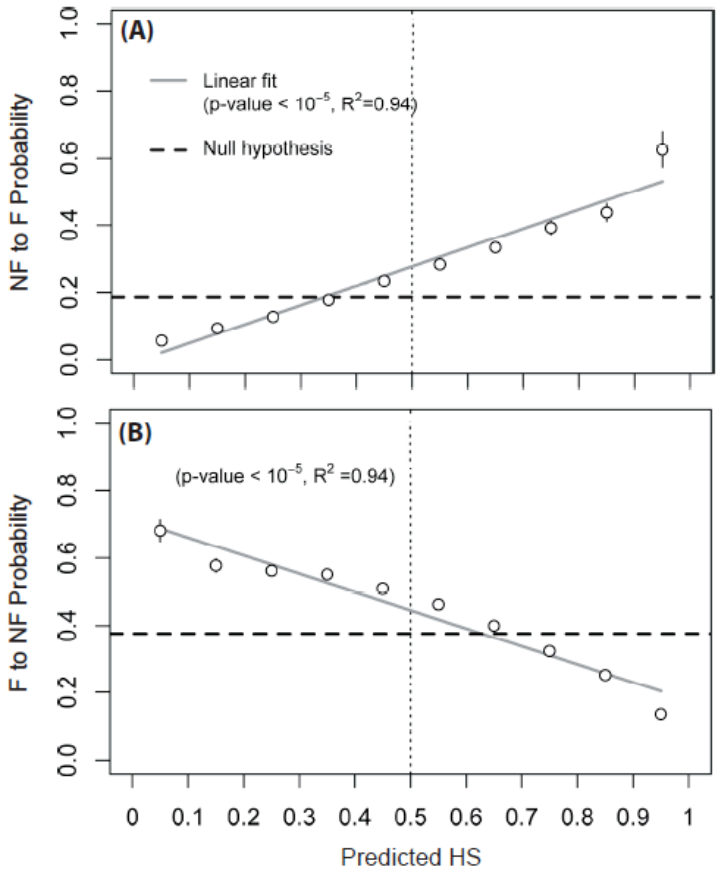


Figure 3.5 (previous page) *Relationships between cell change probabilities and predicted HSI values. The probabilities of forest (F) cell to non-forest (NF) cell changes (and changes in the opposite direction) between 1976 and 2000 are shown as a function of the predicted habitat suitability (HSI). Bars indicate the 95 percent confidence interval and dotted lines show the null hypothesis (i.e. the situation that would be expected if the HSI were independent of the probability of expansion or contraction).*

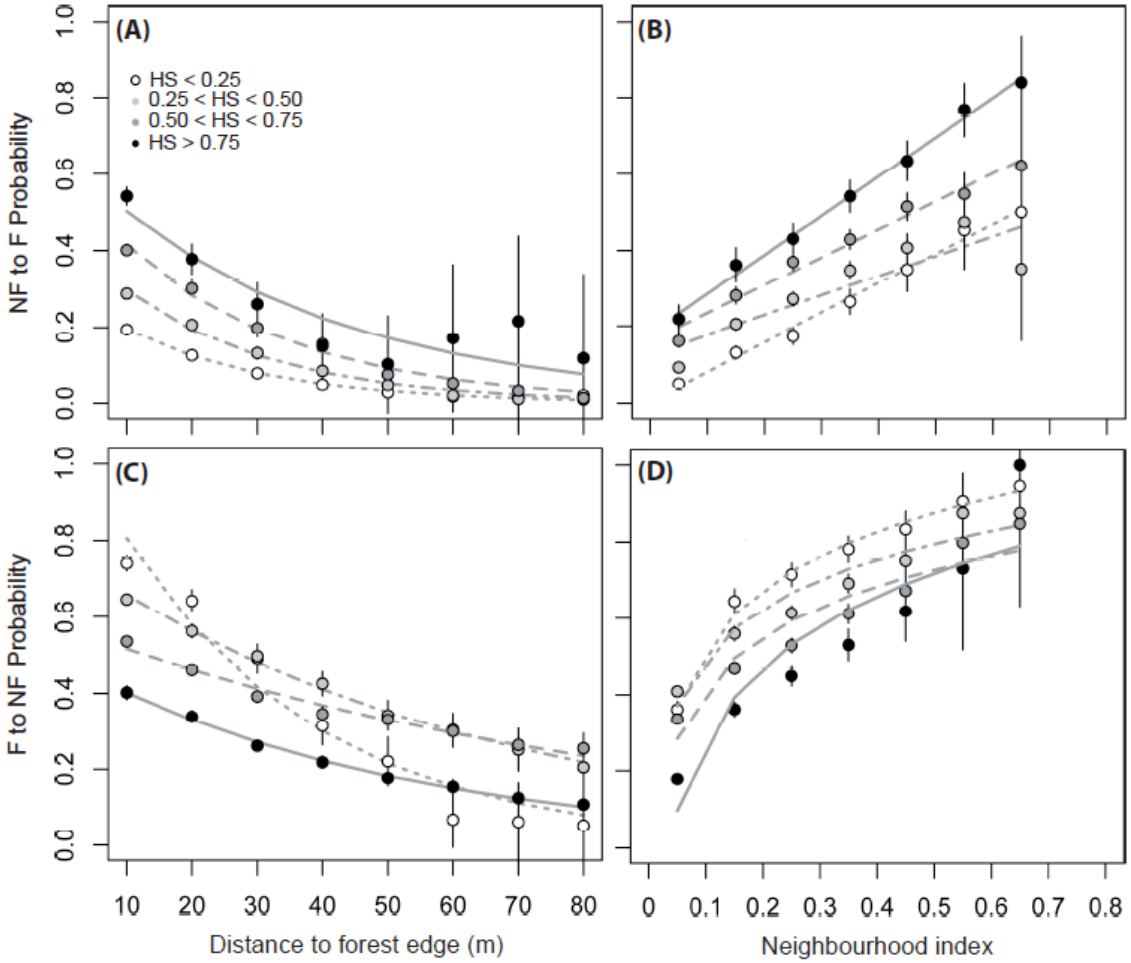


Figure 3.6 *Relationships between cell change probabilities, predicted HSI values, and spatial predictors. Probabilities for the transition of forest (F) cells to non-forest (NF) cells and vice-versa are shown as functions of the cell's distance from the 1976 forest edge (A and C, respectively) and the neighbourhood index (B and D, respectively). Bars indicate the 95 percent confidence intervals. All fitted models (A and C, exponential; B, linear and D logarithmic fit) are significant (p-value < 0.05).*

3.6 Discussion

3.6.1 Forest distribution and exposure to fire

Over the entirety of the studied period (1955-2000), the spatial structure of both the rainforest coverage and of its decreases between 1976 and 2000 were strongly influenced by the topography of the hilly landscape. In the absence of significant grazing and logging pressure, and given that the mean annual precipitation within the region is > 1500 mm, fire was considered most likely to be the main factor controlling the spatial distribution and expansion of savannas, as in other tropical regions (see Bond 2008; Sankaran *et al.* 2004; Staver *et al.* 2011a; Staver *et al.* 2011b).

Topography probably influences the rainforest-savanna distribution and its dynamics in a number of ways, involving both bottom-up control *via* its effects on water and nutrient availability and top-down control *via* its effects on the area's fire regime (Bond 2008). Indeed, topography, ignition events, the availability and nature of the fuel within the region, and the climate interact over time to create spatiotemporal variation in a region's fire regime, in terms of frequency, intensity, extent, type and seasonality (Whelan, 1995). This in turn affects forest coverage and its distribution in the landscape. As such, given that numerous fires are observed within the studied landscape every year by workers conducting anthropological surveys, we assume that anthropogenic fires are the main driver of the observed rainforest-savanna distribution and its dynamics. In this context, the calculated rainforest HSI highlights how interactions between topography and anthropogenic ignition influence a region's fire regime and structure the landscape.

As was done by Brook & Bowman (2006), we have shown that the simulated HSI is a good predictor of both forest presence-absence and forest expansion-contraction. Moreover, our results provide insights into the way that topographic feature, determine the extent to which specific areas are protected from (or exposed to) fire and thus dictate the relative coverage of rainforest and savanna in the hilly landscape of New Caledonia. Aspect was the variable that had the greatest correlation with both forest coverage and its rate of change, with very different responses on east-facing and west-facing slopes. The eastern slopes of the studied region are exposed to

the dominant winds and thus have very low forest coverage, which seems to have already reached its minimum in 1955. Conversely, the west-facing slopes exhibited much greater forest coverage, although it decreased between 1976 and 2000. This result suggests that forest contraction was faster on east facing due to their greater exposure to fire propagation as a consequence of synergistic effects between wind direction and slope. Moreover, the probability of forest expansion on the eastern slopes was also lower, probably as a result of their greater exposure to fire and the generally drier conditions. Forests contraction likely occurred first at lower elevations and gentle slopes where people live; it then progressed upwards, to higher altitudes and steeper slopes. The curvature and the distance to the nearest river are the two other main topographical variables that drive the observed structure and dynamics.

In summary, forests are most resilient in and can expand most easily from areas where fires are rare, *i.e.* along the banks of creeks and in thalwegs where the moisture is high (high HSI), as reported for other tropical locations (Kellman and Meave 1997; Meave *et al.* 1991). On the other hand, forests are vulnerable in places where fire spreads easily, *i.e.* on dry wind-exposed ridges (low HSI). The importance of the distance to the nearest river was previously discussed by Russell-Smith *et al.* (2004a) and Brook & Bowman (2006), but these authors did not mention the aspect effect. We suggest that the differences between the results obtained in those previous studies and our findings are probably due to the combined effect of the smaller areas and more constrained range of elevations examined in the previous studies, both of which would make it harder to observe aspect-related effects. Finally, our results suggest that if environmental and anthropogenic pressure remain constant or become worse (i.e. if ignition events become more common and/or the climate favours more severe fires), west-facing forests will be progressively destroyed by fire, with forests on ridges disappearing first until they are eventually confined to refugia along the banks of creeks and in thalwegs, as appears to have already happened on the east-facing slopes.

Fires are started by the New Caledonian tribal population for a variety of reasons, including pre-cultivation clearing, hunting, the removal of weeds and small fire ants (*Wasmannia auropunctata*), to drive away destructive wild pigs, and also due to social factors such as conflicts (see Appendix II for more information). The spatial distribution of these fire ignitions is determined by accessibility, strong cultural

practices, and land use patterns. We acknowledge that the topography may also have an indirect on fire and forest coverage distribution through its impact on cultural practices and land use pattern. However, we could not extract this indirect effect from the overall effect of topography. Due to their complexity, these variables were not included as HS predictors and therefore induced a low but significant spatial autocorrelation in the models' residuals. Analysis of the HSI residuals thus made it possible to determine that some of the heterogeneous fire pressure stems from a hidden social layer that influences the structure of the landscape (Fig. 4).

For example, one of the large forested areas examined in this work studied was situated in a region with low HSI values and thus gave rise to very high residuals. The persistence of this forest was explained by socio-cultural factors; specifically, the forest is considered "*taboo"* by the tribal population. Taboos and sacred areas of this kind are highly respected in the Kanak culture and thus serve as forest refuges because tribal customs discourage or prohibit entering them and so they are unlikely to be burned.

3.6.2 Forest expansion-contraction and spatial processes

The expansion and contraction of forests is attributable to spatial processes such as seed dispersal or the occurrence and spread of fires. According to Banfai & Bowman (2008), distance from the forest edge is the most important predictor for the probability of change, while fragmentation (neighbourhood composition) is less important. We showed that distance from the forest edge was important, and were able to quantify this importance using the HSI. Indeed, the probability of change was primarily determined by the HSI in cells close to the forest edge (within the first *ca* 30 m); in cells further from the edge, the transition probability was more sensitive to the distance from the edge than to the HSI value. These findings are consistent with previous results concerning distance-constrained diaspore distribution patterns (Clark *et al.* 1999; Nathan and Muller-Landau 2000) and the spread of fires at the edges of tropical forests (Cochrane 2003). Indeed, the first tropical forest fires typically propagate slowly and are low in intensity because they only burn the leaf litter dried by micro-climatic edge effects (see Didham and Lawton 1999; Hennenberg *et al.* 2008). However, these initial fires also modify the structure of the edge and its micro-climatic conditions in a way

that facilitates the occurrence of subsequent fires, allowing them to propagate more rapidly and reach higher intensities (Barlow and Peres 2008; Goldammer 1999). In contrast to Banfai & Bowman (2008), we found that neighbourhood composition (which is a measure of local fragmentation) was also a good predictor of forest expansion-contraction. Indeed, increasing forest fragmentation may increase forest vulnerability to fire by increasing both the number of fire ignitions (usually in savanna patches) and the overall length of the forest-savanna edge (Murcia 1995).

Moreover, forest fragmentation decreases the likelihood of forest expansion by limiting the amount and the proximity of diaspore sources. The arrival of diaspores is a necessary first step in forest recovery in the tropics (Cubina and Aide 2001; Holl *et al.* 2000; Hooper *et al.* 2005). Studies conducted in New Caledonia (Bocquet *et al.* 2007; Carpenter *et al.* 2003) and many other tropical locations (Arteaga *et al.* 2006; Gonzales *et al.* 2009) have highlighted the importance of dispersal by birds and bats. Rainforest fragmentation and the low attractiveness of savannas may both limit seed arrival and slow down rainforest recovery by affecting the behaviour of these important dispersers (Arteaga *et al.* 2006; Herrera and Garcia 2010; Holl *et al.* 2000; Levey *et al.* 2005).

3.6.3 Environmental changes, fire regime and landscape forest coverage

To our knowledge, there is little available historical data on fire regimes in New Caledonia aside from that gathered through paleoecological studies and ongoing remote sensing analyses. However, on the basis of ongoing remote sensing analyses and field observations, we hypothesise that over the last 50 years, environmental and anthropogenic changes that affected fuel availability and ignition events changed the fire regime in a way that accelerated the decrease in forest coverage.

Fire regime can be altered by long-term changes in the quantity, quality and / or spatial arrangement of fuels induced by changes in the nature and quantity of vegetation at a given site. As such, modifications of the composition of the savanna ground layer following the arrival of invasive weeds may also partly explain the observed reduction in forest coverage. Indeed, invasive weeds, which have been introduced on a massive and increasing scale since *ca* 1950, are often dominant in degraded New Caledonian landscapes (Gargominy et al. 1996). In the studied landscape, invasive weeds such as

Lantana camara L. and *Melinis minutiflora* Beauv. often dominate the savanna ground layer and have particular fuel properties (*i.e.* load, structure, and perhaps flammability) that may promote the occurrence and propagation of fires (Brooks *et al.* 2004; Mack and D'Antonio 1998), thereby increasing the vulnerability of forest edges (Hoffmann et al. 2004).

It is likely that environmental, social and cultural changes over time have adjusted fire ignition practices and disturbed the rainforest-savanna equilibrium. While we are not aware of any published studies on this topic, local agencies recognize that there are some ongoing changes that influence factors related to ignition events (De Garine and Lepoutre-Goffinet 2004). These changes include the introduction of invasive species and socio-cultural transformations, both of which seem to be increasing the frequency and the seasonality of fires. For example, the tribal population sometimes sets fires to clear areas of invasive weeds, to drive out wild European wild pigs (*Sus scrofa*), which devastate crops, or to facilitate the hunting of invasive deer (*Cervus timorensis russa*). Moreover, it seems that during the dry season, fire is used more extensively and in a relatively uncontrolled fashion to prepare and maintain croplands.

Rainfall anomalies related to *El Niño* / *La Niña* have strong effects on the spatiotemporal variability of fire regimes on global and regional scales (Fuller and Murphy 2006; van der Werf *et al.* 2008a). However, we did not observe any significant correlation between the rate of change of forest coverage and climate (in terms of volume of precipitation or temperature anomalies; data not shown). We suggest that our data may be insufficient to identify such relationships because of the irregularity with which the aerial photographs had been acquired and bias introduced by the timing of the photography sessions relative to the successive *El Niño* and *La Niña* events that would have occurred in the intervening years. Nevertheless, it is interesting that the highest observed rate of rainforest contraction (*ca* 35 ha / yr) occurred during 1997-2000 and may have been linked to the 1997-1998 *El Niño* event, as was the case for forest losses in other tropical locations (Barlow and Peres 2008; Siegert *et al.* 2001).

Environmental and associated fire regime changes affect rainforest coverage by directly affecting forest, but they also have indirect effects in that they can limit or slow the post-fire recovery of the forest. The key processes involved in forest expansion or secondary succession are diaspore arrival, germination, growth, and survival of forest

species in savanna. While the primary limitations on diaspore arrival are spatial in nature, the germination, growth and survival of forest species in savannas are limited by a range of different biological and physical factors, the most important of which are competition with savannas species and fires. It has previously been reported that several factors limit the successful establishment of forest seedlings, including competition with grass cover, microclimate, water stress, and nutrient supplies (Hoffmann *et al.* 2004; Holl *et al.* 2000) and grazing (De Garine-Wichatitsky et al. 2005). Because weeds can inhibit tree regeneration (Dantonio and Vitousek 1992; Hoffmann and Haridasan 2008), the dominance of the ground layer of the savanna by invasive weeds may also be an important factor that limits forest recovery in the studied landscape (Aide and Cavelier 1994). However, given the high fire pressure observed in the area, and the fact that forest species are generally less able to survive fire than are savanna species (Hoffmann et al. 2003), it seems likely that fire is the main factor that limits the success of forest species in savannas (Hoffmann et al. 2004).

3.6.4 Conclusion

The analysis presented in this paper represents the first detailed examination of the structure and dynamics of rainforest-savanna landscapes at intermediate altitudes in New Caledonia. Our results indicate that most areas on east-facing slopes have already undergone a transition to the stable savanna state; the only exceptions occur along thalwegs and by the banks of creeks, in which environments the rainforest has proven more resilient. A similar shift appears to be in progress on the west-facing slopes. Our results suggest that, rainforests on west-facing slopes will be progressively destroyed by fire until the only remnants of their presence are isolated patches of rainforest in refuges, as appears to have already happened on the east-facing slopes. The end result of this process may be a new and stable landscape-scale rainforest-savanna mosaic similar to that described by Perry and Enright (2002a) for ultramafic areas with a rainforest-maquis mosaic.

As in many places in the Tropics, Humans are the main source of fire ignition (Stott 2000), thus cultural and land use patterns are likely with topography the main drivers of rainforest distribution. We partially pointed out this anthropogenic

component by analysing the residuals of the HSI model. However, topography may also influence ignition patterns but we didn't have enough knowledge to extract this indirect effect of topography from its direct effect on fire behaviour. Finally, we could expect that anthropogenic fire pressure could decrease due to demographic or socio-cultural changes, and in such case, forest would expand on savanna following the HSI gradient.

Our results raise questions that are of general relevance to tropical forest remnants, concerning (1) their sustainability under fire pressure and in the face of extreme climatic events (2) their biological and functional diversity and (3) their capacity for expansion in the event that the fire pressure were to be somehow reduced. The resilience of the rainforest (in terms of coverage and biodiversity) will likely depend on the amount, the quality, and the functional diversity of the remnant forests.

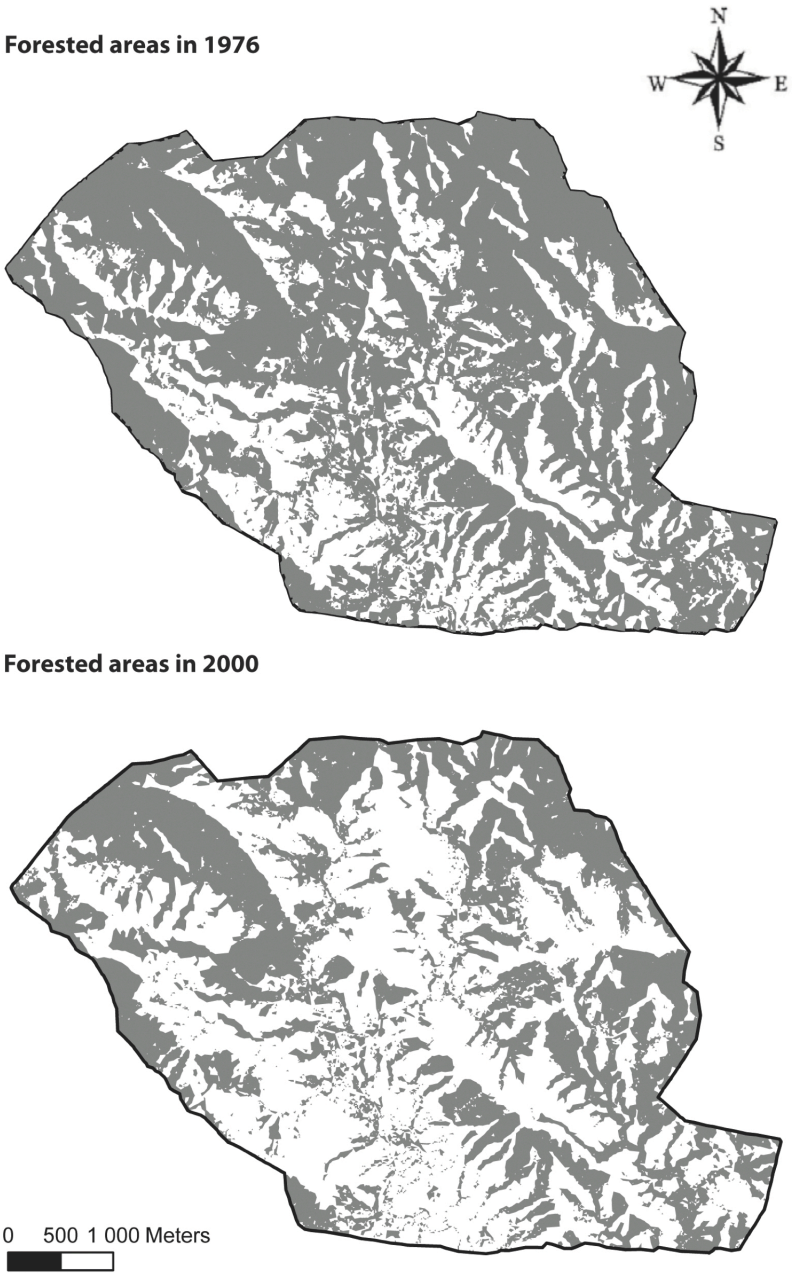
Weeds and invasive mammals cause increased anthropogenic fire ignition and thereby alter the area's fire regime, disfavouring seedling survival and growth. As such, it appears that these factors, along with social changes, have a significant effect on the loss of the New Caledonian rainforests. The results presented herein demonstrate that HSI maps can provide an effective "*index of topographic fire protection*" and are thus likely to be useful for the restoration and management of forests in the studied region and elsewhere.

3.7 Acknowledgements

We thank the ANR BDIV-07-008 project INC and the CNRS for funding this research and the PhD scholarship of T. Ibanez, the *Direction des Infrastructures de la Topographie et des Transports Terrestres* of New Caledonia for providing aerial photographs, the *Direction des Technologies et Services de l'Information* of New Caledonia for providing the Digital Elevation Model.

3.8 Appendix

Appendix I : *Maps of forest coverage in 1976 and 2000*



Appendix II : *Fire use*

This appendix presents supplementary material, which was not present in the original submitted paper. A trainee in ethno-ecology (Nathalie Udo), which I co-supervised, has obtained these results (Udo 2011).

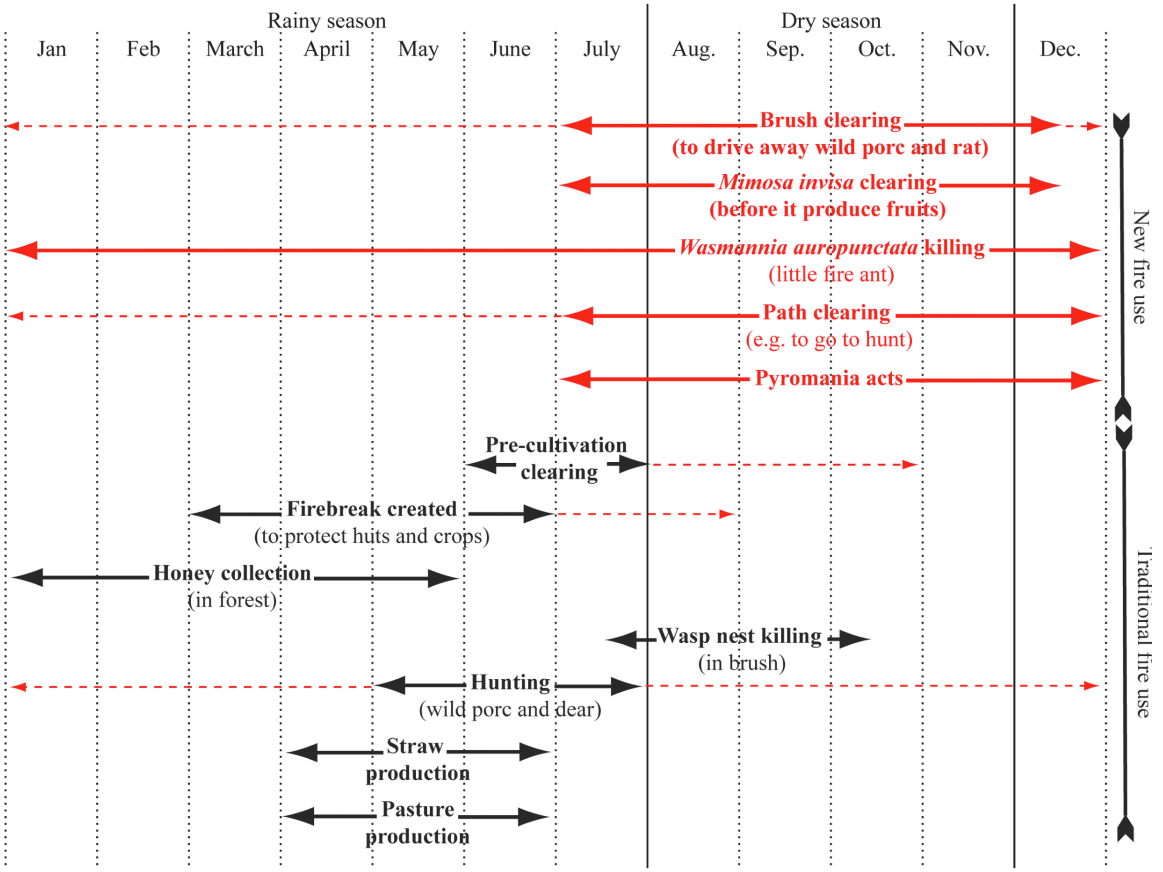


Figure 3.7 *Seasonality of Kanak's fire use in the studied region. Traditional fire uses are represented in black while new ones are represented in red. Arrows with full lines represent the main seasons of the fire use dotted ones represent extensions of the main season.*

This calendar points out three important results (Figure 3.7). Firstly, new fire use had likely emerged with environmental changes and the development within the studied landscapes of invasive species. Fire is used widely by Kanaks to clean areas invaded by weeds such as *Mimosa invisa*, *Melinis minutiflora* or *Lantana camara* and to drive away wild pigs (*Sus scrofa*) or rats (*Rattus exulans* and *R. rattus*), which devastate their cultivation. Secondly, contrarily to traditional practices, for which fire is mainly used

before the dry season, these new practices occurred mainly during the dry season, which likely conduce to more uncontrolled wild fire. Thirdly, due to socio-economical changes, there are also changes in the seasonality of traditional fire use such as pre-cultivation clearing. Fires lighted to clean crops are easier to control before the dry season but during the dry season these fires often conduce to uncontrolled wildfire.

Chapitre II

Résumé du chapitre

Une modification du régime d'incendies dans les savanes (baisse de leurs fréquences) peu permettre la mise en place de successions secondaires et *in fine* la conversion de zones de savanes en formations forestières secondaires. Le second chapitre de cette thèse étudie la structure et la composition de ces formations secondaires ainsi que les principales barrières à leurs établissements (i) mortalité post incendie, (ii) apport de graines et (iii) compétition avec les espèces invasives.

Dans la première section (section 4) de ce chapitre différents modèles de successions secondaires (formations mixtes et formations mono-dominantes à *Codia albicans*) ont été mis en avant à partir de relevés floristiques. Les travaux effectués dans cette section ont permis d'identifier différents cortèges d'espèces pionnières, post-pionnières et forestières et de préciser leurs écologies. Dans une seconde section (section 5), la structure spatiale de ces formations secondaires a été étudiée afin de mettre en avant les processus de dispersion, de compétition ou de facilitation mis en jeux lors de la succession secondaire. Ces analyses ont notamment permis d'analyser la mortalité des arbres de savanes (les Niaoulis, *Melaleuca quinquenervia*) au cours des successions secondaires.

Dans une troisième (section 6) et quatrième section (section 7) la tolérance aux incendies des espèces pionnière identifiées dans la première section et des arbres de savanes a été analysé en utilisant une combinaison de mesures de traits fonctionnelles, de modélisation du comportement des feux de savanes et d'estimation des dommages potentiels associés. Ces section ont permis de mettre en avant que le Niaoulis (*M. quinquenervia*), l'arbre dominant les savanes néo-calédoniennes présente une forte tolérance aux incendies (notamment grâce à une écorce épaisse et une capacité de rejet précoce) alors que les principales espèces pionnières identifiées y présentent une faible tolérance.

Enfin dans les deux dernières sections de ce chapitre, les deux autres principales barrières potentielles au développement de succession secondaires en savanes ont été explorées. Dans les zones très fragmentées, le faible apport de graines en savanes semble être une barrière importante à l'installation de succession secondaires (section 8). Il semblerait toutefois que cette barrière puisse être surmontée par effet perchoir en

promouvant l'installation d'arbres attractifs pour les disperseurs de graines (oiseaux, chauves-souris). Le succès d'installations des espèces pionnières en savanes semble aussi limité par la compétition avec les espèces invasives (*e.g. Lantana camara*) très presentes sur le site d'étude (section 9).

Ainsi, dans les zones fragmentées, le faible apport de graine, la forte compétition avec les herbacées invasives, la faible tolérance aux incendies des espèces pionnières semble rendre très difficile le développement de succession secondaire sans l'intervention de l'Homme (gestion des incendies et des espèces invasives et restauration active).

4 Mono-dominated and co-dominated early secondary succession patterns in New Caledonia

This section is submitted (since June 6th 2011) to *Biotropica* as the following research paper :

Ibanez, T., Munzinger, J., Géraux, H., Gaucherel, C., and Hély, C., (submitted). Mono-dominated and co-dominated early secondary succession patterns in New Caledonia, submitted to *Biotropica*.

4.1 Résumé

La perte d'habitat est l'une des principales causes de l'actuelle crise de biodiversité. Comprendre les processus de successions secondaires qui permettent à la forêt de croître naturellement dans des écosystèmes perturbés est un enjeu majeur pour la restauration de la biodiversité et des services éco-systémiques. La première analyse des stades précoces de la succession secondaire de la savane vers la forêt dense humide sur roches acides en Nouvelle-Calédonie est présentée dans cette étude. Une combinaison originale de données de terrain et de données d'herbiers a été utilisée pour analyser les différentes compositions d'espèces pionnières et les modèles de successions associées. Une liste des principales espèces pionnières identifiées et candidates potentielles pour la restauration forestière est proposée et deux différents modèles de succession secondaire ont été identifies. Le premier modèle correspond à des formations mono-dominantes dominées par une espèce anémochore (*Codia albicans*) qui semble conduire à une rapide fermeture de la canopée mais à un lent retour de la diversité d'arbre. Le second correspond à des formations mixtes, co-dominées par des espèces anémochores (*Geissois racemosa* and *Alstonia costata*) et ornithochores (telles que *Guioa villosa* et *Pittosporum simsonii*) qui semble conduire à une fermeture de la canopée plus lente mais à retour plus rapide de la diversité d'arbre.

Mots clés: Analyse de communauté, extension forestière, données d'herbier, forêt dense humide, savane.

4.2 Abstract

Habitat loss is one of the main causes of the current biodiversity crisis. Understanding the secondary successional processes that allow forest to expand into disturbed ecosystems is critical to restore forest biodiversity and ecosystems services. The first analysis of the early secondary successional stages from savanna to rainforest on acidic rocks in the New Caledonian biodiversity hotspot was provided in this study. A combination of field sampling and herbarium data (specimens' locations and associated ecological data) was used to analyse pioneer species composition and associated patterns of secondary succession. A short list of main pioneer species and potential candidates for forest restoration was proposed and two different patterns of secondary succession were identified. Firstly, mono-dominated formation dominated by a wind-dispersed species (*Codia albicans*) that likely leads to a rapid closure of the canopy but a slow tree diversity recovery. Secondly, a mixed formation co-dominated by wind-dispersed species (*Geissois racemosa* and *Alstonia costata*) and bird-dispersed species (such as *Guioa villosa* and *Pittosporum simsonii*) that likely leads to a slower closure of the canopy but a faster tree diversity recovery. These first results on secondary succession from savanna to rainforest have strong implications for forest restoration in New Caledonia.

Keywords: Community analysis; forest expansion; herbarium data; rainforest; savanna.

4.3 Introduction

Habitat loss is one of the main causes of the current biodiversity crisis (Brooks *et al.* 2002; Wright and Muller-Landau 2006a) and global rate of forest habitat destruction is still alarmingly high (FAO 2010). Thus, understanding the natural secondary successional processes that allow forest to expand into disturbed ecosystems is critical to accelerate forest recovery by restoration (Lamb *et al.* 2005) to preserve and restore forest biodiversity and ecosystems services. Indeed, the successful restoration of a disturbed ecosystem depends on its understanding (Bradshaw 1987). In this context, the aim of successional ecology is to describe patterns and understand processes associated with natural changes in vegetation composition along time, in response to external changes or disturbances such as fire regime changes (see McCook 1994). The aim of the present work is to study secondary succession using field sampling and herbarium data.

Myers (1988) initially identified ten tropical forest hotspots, including New Caledonia (NC), characterised by both exceptional levels of plant endemism and serious levels of habitat loss. With less than 30 percent of the *ca* 19.000-km^2 of original vegetation remaining and an exceptional biodiversity (vascular plant flora comprise ca 3500 taxa with close to 75 percent of endemism, Jaffré *et al.* 2001) inherited from a particular geological history (Grandcolas *et al.* 2008), NC is the smallest of the 34-revisited biodiversity hotspots defined for conservation priorities (Mittermeier *et al.* 2004; Myers *et al.* 2000). Jaffré *et al.* (1998) identified four native vegetation types from an ecological and conservation perspective : rainforest, dry forest (below 300 m asl and on areas receiving less than 1100 mm rainfalls per year, and outside ultramafic substrate), low and middle elevation maquis, and high elevation maquis.

Three main types of rainforest defined by edaphic substrates were identified by Jaffré et al. (2009): rainforest on ultramafic (“terrain minier”), acidic (volcano sedimentary) and calcareous rocks. The main threat for the NC forests and their biodiversity are mining activities on ultramafic rocks, anthropogenic bush fires and invasive plant and animal species (Jaffré *et al.* 1998; Pascal *et al.* 2008).

Since the arrivals of Melanesian (*ca* 3000 yr BP), and particularly since the European settlement on the island (in the mid-1800s), a great part of the NC native forests have been replaced by open anthropogenic formations (Hope and Pask 1998;

McCoy *et al.* 1999; Stevenson 2004), mainly maquis on ultramafic rocks, and savanna and secondary thicket on non-ultramafic rocks (Jaffré *et al.* 1998). Today these secondary formations, such as savannas that cover almost 30 percent of the main island, are maintained by disturbances such as bush fires and grazing (Jaffré and Veillon 1994). However, under lower disturbance regimes processes of secondary succession allow woody species to naturally expand and to reconstruct woodland and forest on open anthropogenic formation. To our knowledge, such successional processes have been studied in NC for (1) the secondary succession from savanna to dry forest (Bocquet *et al.* 2007; Jaffré *et al.* 1997b) and (2) the secondary succession from maquis to rainforest on ultramafic substrates (Enright *et al.* 2001; Jaffré *et al.* 1997b; McCoy *et al.* 1999), while the secondary succession from savanna to rainforest on non-ultramafic substrates, although critical for forest restoration, has retained less interest.

Secondary forest succession studies often consist in analyzing the composition and structure of secondary forest stands using field sampling and ordination statistical techniques (e.g. Liebsch *et al.* 2008; Pena-Claros 2003). Field sampling can be labour-intensive, time consuming and makes broad-scale studies difficult. However, an alternative is the use of herbarium data that allows scientists to take advantage of the efforts of other collectors (Garcillan and Ezcurra 2011). As suggested by Crawford & Hoagland (2009) we chose "*to take advantage of information gathered by the scores of botanists before us and to design novel techniques and new avenues of research utilizing herbarium records*". Herbariums are indeed great sources of ecological data (*e.g.* the herbarium of Nouméa, NOU's database (VIROT) contains *ca* 85.000 specimens of which 90 % are from NC).

Modernization of herbariums with the digitisation and the creation of electronic database like NOU's database (VIROT) have enhanced their accessibility and facilitated the research of data *via* database software and their request tools. Thus, herbarium data are widely used in broad-scale biogeographical studies, using the localisations of known specimens, to analyse species distribution (e.g. Linares-Palomino and Kessler 2009; Loiselle *et al.* 2008) and to map species richness (e.g. Kalema 2008; Raedig *et al.* 2010). However, to our knowledge, environmental data associated to specimens localisations have been less or not used in the literature.

In this paper we analysed the early secondary successional stages from savanna to rainforest on acidic rocks in NC to identify common pioneer species composition and associated patterns of secondary succession. We hypothesized that differences among patterns of secondary succession were driven by differences in the ecology (dispersal abilities and shade tolerance) of earlier pioneer species. We used field sampling and community analysis to identify patterns of secondary succession in a savanna-rainforest mosaic landscape, associated to herbarium data to analyse the ecology of identified pioneer species at the New Caledonia scale.

4.4 Materials and methods

4.4.1 Study area

The New Caledonia (NC) archipelago is a French overseas territory located in the south-western Pacific inter-tropical zone, close to the Tropic of Capricorn (20°-23°S and 164°-167°E, Figure 4.1). The climate is tropical oceanic with a cool and a hot season, both overlapping with a characteristic dry season.

New Caledonian rainforest covers *ca* 3800 km^2 (1800 km^2 on acidic rocks versus 1100 and 900 km^2 on ultramafic and calcareous rocks, respectively) in areas receiving rainfall from 1300 to more than 3500 mm / yr (Jaffré *et al.* 2009). Rainforest is rare and fragmented at low and middle elevation, and therefore restricted to high elevation or inaccessible areas along the central mountain chain (Jaffré *et al.* 1998; Jaffré and Veillon 1994).

Field sampling was realised at the interface of the west coast savannas and central mountain chain rainforest, on the foothill (between *ca* 100-650 m asl) of the western side of the *Aoupinié* mountain (1006 m asl, 21°11'S and 165°15'E). The *Aoupinié* mountain is located in the middle of New Caledonia's main island ("*Grande Terre*") and shelters one of the greatest rainforest on acidic rocks, mostly included in a protected area. Rainfall ranges from 1500 to 3000 mm / yr (METEO-France 2007).

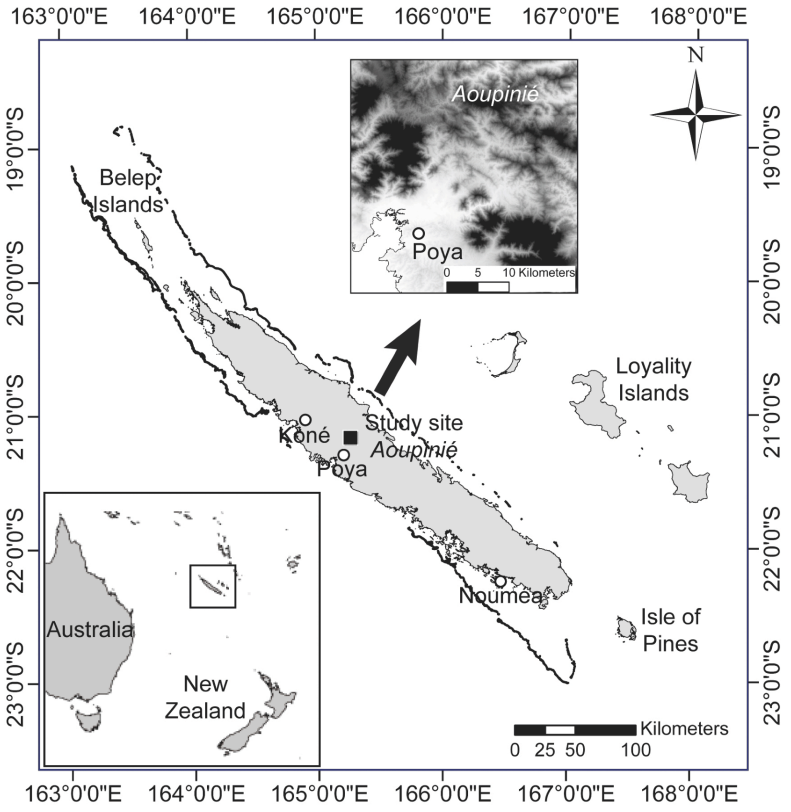


Figure 4.1 *Location of the studied area. Field sampling were performed on the western side of the Aoupinié mountain (1006 m) in the middle of the New Caledonia main island. Specimens from all New Caledonian localities were taken into account for the herbarium data analysis.*

4.4.2 Inventory

Botanical survey was performed on 29 sites of different sizes (from 100 m^2 to 1500 m^2 for a total of 10.400 m^2) as reflecting the occurrence of secondary formations (Table 4.1). Two indicators were used to identify secondary formations for site selection. Firstly we used a temporal aerial photography analysis to identify potential areas of savanna re-colonization by forest. Secondly, as *Melaleuca quinquenervia* (Cav.) S.T. Blake (locally known as "*niaouli*") is the dominant tree species of New Caledonian savanna and is a shade intolerant species, its presence (dead or alive) was used as a bio-indicator of the presence of savanna on the site before tree colonization and the canopy

Table 4.1 *Sampling description.*

Site	Sampled area (m^2)	Nb. of stems	Stem density (stems / 100 m^2)	Basal area (m^2 / 100 m^2)	Level of identification (%)				Diversity	
					NI	Family	Genus	Species	Nb. of *taxa*	H'
1	400	62	16	0.50	1.6	6.5	24.2	67.7	17	1.19
2	400	97	24	0.21	-	-	-	100.0	7	0.54
3	200	48	24	0.24	-	-	4.2	95.8	8	0.64
4	400	102	26	0.32	-	-	7.8	92.2	23	1.00
5	400	71	18	0.53	2.8	-	19.7	77.5	24	1.27
6	100	30	30	0.33	-	-	-	100.0	5	0.59
7	200	42	21	0.26	-	-	11.9	88.1	11	0.88
8	200	77	39	0.23	-	-	1.3	98.7	12	0.76
9	400	69	17	0.33	4.3	-	14.9	80.9	15	1.02
10	200	45	23	0.47	-	-	15.6	84.4	9	0.66
11	200	49	25	0.63	-	-	-	100.0	6	0.24
12	100	34	34	0.36	-	2.9	-	97.1	6	0.62
13	400	130	33	0.44	-	1.5	-	98.5	8	0.42
14	200	58	29	0.31	-	-	-	100.0	5	0.18
15	200	41	21	0.39	2.4	-	-	97.6	8	0.77
16	100	45	45	0.63	-	2.1	6.4	91.5	10	0.86

17	400	68	17	0.35	-	-	5.9	94.1	16	1.05
18	200	54	27	0.34	-	-	5.6	94.4	7	0.50
19	400	91	23	0.38	-	-	6.6	93.4	18	0.89
20	400	52	13	0.34	-	-	7.6	92.5	13	0.95
21	200	30	15	0.12	-	-	-	100.0	7	0.66
22	200	16	8	0.26	-	-	62.5	37.5	7	0.76
23	200	59	30	0.33	23.7	-	1.7	74.6	10	0.88
24	200	37	19	0.39	2.7	-	0.0	97.3	14	1.02
25	400	121	30	0.62	11.5	3.3	4.1	81.2	11	0.82
26	1500	278	19	0.35	-	0.4	14.4	85.3	22	0.95
27	900	100	11	0.21	-	-	4.0	96.0	12	0.64
28	400	109	27	0.57	3.3	-	15.7	81.0	14	0.61
29	900	378	42	0.48	5.3	-	0.5	94.2	6	0.29
Total	10400	2393	24	0.38	2.4	0.5	6.7	90.4	77	0.75

closure of the site (see Serbesoff-King 2003 for more details on the ecology of *Melaleuca quinquenervia*).

In selected sites all trees with diameter at breast height (DBH, at 1.3 m) ≥ 5 cm were marked and their DBH were recorded. Seedlings taller than 20 cm were also inventoried in 21 of the 29 sites (*i.e.* all but the sites 22 to 29) in sub-plots in order to cover 10 percent of the plot. Samples were identified at the herbarium of the centre IRD of Noumea (NOU) using the New Caledonian flora (Aubréville *et al.* 1967-present) and identified material. Identified samples have been deposited at NOU and unidentified ones were given morphospecies names. For each site we computed the number of trees with DBH ≥ 5 cm, the tree density, the basal area, the number of *taxa*, the levels of identification (*i.e.* at the species, genus or family levels, or not identified) and the log10 Shannon-Weaver diversity index.

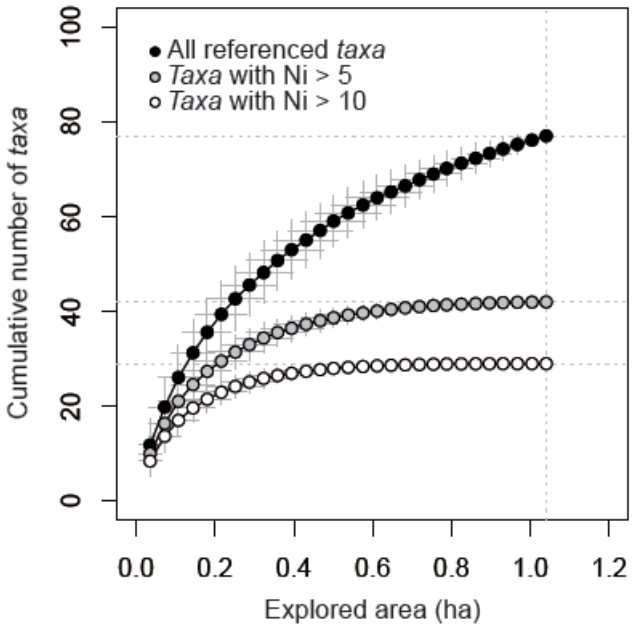


Figure 4.2 *Cumulative number of taxa referenced against the explored area. Grey bars represent 95 percent confident intervals obtained by bootstrap (with 1000 iterations).*

Along the 29 sample sites 2393 trees were inventoried (Table 4.1). Tree density ranged from 8 to 45 stems / 100 m^2 (mean = 24 ± 9) and basal area ranged from 0.12 to 0.63 m^2 / 100 m^2 (mean = 0.38 ± 0.13). We identified *ca* 90 and 95 percent of the inventoried trees at species and genus levels respectively for a total of 77 *taxa* identified

Table 4.2 *Taxa represented by more than 10 individuals along the field sampling. The 24 first, identifies at the species level were used in data analysis.*

Family	Scientific name	Status[a]	Number of individuals (%)		Number of sites (%)	
Cunoniaceae	*Codia albicans* Vieill.	EE	714	(29.8)	8	(27.6)
Myrtaceae	*Melaleuca quinquenervia* (Cav.) S.T. Blake	A	320	(13.4)	23	(79.3)
Sapindaceae	*Guioa villosa* Radlk.	E	163	(6.8)	19	(65.5)
Cunoniaceae	*Geissois racemosa* Labill.	E	126	(5.3)	13	(44.8)
Sapindaceae	*Elattostachys apetala* (Labill.) Radlk.	A	118	(4.9)	15	(51.7)
Rutaceae	*Acronychia laevis* Forster & G. Forster	A	92	(3.8)	19	(65.5)
Pittosporaceae	*Pittosporum simsonii* Montrouz.	E	90	(3.8)	12	(41.4)
Apocynaceae	*Alstonia costata* (G. Forster) R. Brown	E	88	(3.7)	11	(37.9)
Apocynaceae	*Pagiantha cerifera* (Pancher & Sebert) Markgraf	E	45	(1.9)	11	(37.9)
Ebenaceae	*Diospyros fasciculosa* (F. Muell.) Fmuell.	A	42	(1.8)	10	(34.5)
Euphorbiaceae	*Codiaeum peltatum* (Labill.) P.S. Green.	A	42	(1.8)	4	(13.8)
Loganiaceae	*Fagraea berteroana* A. Gray	A	38	(1.6)	15	(51.7)
Bigoniaceae	*Deplanchea speciosa* Vieill.	E	22	(0.9)	5	(17.2)
Oleaceae	*Olea paniculata* R. Br.	A	22	(0.9)	4	(13.8)
Epacridaceae	*Styphelia cymbulae* (Labill.) Spengel	A	21	(0.9)	3	(10.3)
Euphorbiaceae	*Glochidion billardieri* Baill.	E	21	(0.9)	5	(17.2)

Cyatheaceae	*Cyathea veillardii* Mett.	A	19	(0.8)	5	(17.2)
Rubiaceae	*Gardenia oudiepe* Vieill.	E	18	(0.8)	3	(10.3)
Moraceae	*Ficus habrophylla* Bennett ex Seemann	A	18	(0.8)	8	(27.6)
Araliaceae	*Schefflera gabriellae* Baill.	E	16	(0.7)	4	(13.8)
Euphorbiaceae	*Glochidion caledonicum* Baill.	E	14	(0.6)	6	(20.7)
Bischofiaceae	*Bischofia javanica* Blume	A	12	(0.5)	6	(20.7)
Meliaceae	*Dysoxylum roseum* C. DC.	E	11	(0.5)	2	(6.9)
Mimosaceae	*Archidendropsis fulgens* (Labill.) Nielsen	E	10	(0.4)	3	(10.3)
Sapindaceae	*Cupaniopsis spp*	E	52	(2.2)	12	(41.4)
Araliaceae	*Schefflera spp*	E	14	(0.6)	4	(13.8)
Araliaceae	*Meryta spp*	E	13	(0.5)	5	(17.2)
Clusiaceae	*Garcinia spp*	E	13	(0.5)	9	(31.0)
Lauraceae	*Cryptocarya spp*	E	13	(0.5)	5	(17.2)

[a] EE for endemic genus. E for endemic species and A for authoctonous species

at least at the genus levels (see Appendix). Dealing with all referenced *taxa*, the sampled area was too small to reach the plateau of the curve of the cumulative number of *taxa* against the explored area (Figure 4.2). However dealing with *taxa* showing more than 10 individuals on the sampled area, a plateau at 29 cumulated *taxa* was reached. This subsample of 29 *taxa* (Table 4.2) represented more than 90 percent of the total inventoried trees. Among these 29 *taxa*, 24 were identified at the species level and used in the data analysis, while the five remaining were identified at the genus level and used as supplementary material. We determined the dispersal syndrome (dispersal by wind, bird and bat or another agent) of the main early pioneer species identified by analysing fruit type and seed morphology.

4.4.3 Herbarium data

For each of the 24 species used in data analysis, we extracted in the NOU's database (VIROT) a list of all specimens known in order to compute their location and their distribution in different formation types. A total of 708 herbarium specimens were extracted with on average 30 specimens per species (min = 6, max = 119, sd = 25). The collector's comments allowed us to determine in which formation the latter have been collected. Ten formation types within three groups were retained (1) the closed formation group with rainforest, (2) the semi-open formations group with secondary forest, gallery forest, dry forest and forest edges and, (3) the open formations group with savanna, secondary vegetation, maquis and swampy areas. The total number of specimens collected from these different formations was highly variable. More than 35 and 15 percent of the specimens were collected in rainforest and gallery forest, respectively. Moreover, although species were selected into a savanna-rainforest dynamics context, *ca* 20 percent of the specimens were collected in maquis against only *ca* two percent in savanna.

Among these 24 species, we also computed the location of the specimens identified as dominant species of early secondary successional forest, to identify the range of edaphic substrates (ultramafic, acidic or calcareous rocks) and elevations at which these species are present. Thus, we completed our dataset by adding specimens that were not in NOU, from Paris herbarium (P), downloading information from

SONNERAT (http://coldb.mnhn.fr/colweb/form.do?model=SONNERAT/) and from Missouri Botanical garden (MO) database TROPICOS (http://www.tropicos.org/). This list was completed again by checking on taxonomic revision of the list of material, for the different species: *Guioa* (van Welzen 1989), *Alstonia* (Sidiyasa 1998), *Pittosporum* (Tirel and Veillon 2002), *Glochidion* (McPherson 1991), *Tabernaemontana* (*Pagiantha*) (Boiteau 1981). Finally, we added all available data on these species obtained during botanical inventory at the Botanical Laboratory of Nouméa (observations without herbarium specimens). The geographic coordinates of old specimens were given using the MacKee collection's gazetteer (http://www2.mnhn.fr/novcal/index-georeference-de-prospection-botanique.html) or using New Caledonian maps.

4.4.4 Analyses

To highlight species association we conduced factorial correspondence analysis (FCA) on the table of the 24 species' relative importance values against the sites using the R package *ade4* (Dray and Dufour 2004). Relative importance values (RIV) were computed for each species in each site as [(RSD+RBA) / 2] * 100, where RSD is the relative stem density and RBA is the relative basal area. Before computing FCA, RIV were square root transformed in order to reduce the importance of dominant species.

In order to identify the main species association patterns we performed a cluster analysis using hierarchical ascendant classification (HAC) and Ward's grouping method of plots according to their coordinates on the FCA's two first axis and using the R package *cluster*. The number of cluster groups, determined by the dendrogram's cutting level was graphically selected on the curve of the remaining height against the number of clusters. We assessed the significance of the difference between clustered groups using a similarity test (ANOSIM) and the produced R statistic ranging from zero (no group-discrimination) to one (complete discrimination among groups).

We determined the number of dominant species of each site using a dominance analysis (Ohtsuka 1999) based on the RIV. In a community dominated by a single species, its RIV may be stated at 100 percent but if two species are co-dominant, the RIV of each should ideally be 50 percent, if three species are co-dominant their

expected RIV is 33.3 percent and so on. The number of dominant species was that showing the least deviation between the actual RIV and the expected percentages share of the corresponding co-dominant-number model (Kikvidze and Ohsawa 2002). This deviation (d) was calculated with the following equation:

$$d = \frac{1}{N}\left\{\sum_{i \in T}^{n}(x_i - x')^2 + \sum_{i \in U}^{n} x_j{}^2\right\}$$

where x_i is the actual percentage share (RIV_i) of the top species i (T, *i.e.* in the top dominant of the one-dominant model, or the two top dominants in the two-dominants model, and so on), x' is the ideal percentage share based on the model as mentioned above, and x_j the percentage share of the remaining of the top species (U) and N the total number of species. We only considered species as co-dominant species if there were 5 or less co-dominant species (*i.e.* RIV = *ca* 20 percent for each co dominant species). All statistical analysis were performed using the R 2.9.2 environment for statistical computing (R Development Core Team 2009).

4.5 Results

4.5.1 Floristic groups reflecting successional patterns

FCA associated to HAC highlighted three groups of sites (Figure 4.3). On the first axis of the FCA, floristic composition clearly discriminated sites widely dominated by *Codia albicans* (Group II with eight sites) and sites where *Codia albicans* was not recorded (Groups I and III with two and 18 sites, respectively). On the second axis, sites co-dominated by *Melaleuca quinquenervia*, the savanna dominant tree species (Group I), were neatly opposed to the sites where conversely, *Melaleuca quinquenervia* was rare (Group III).

These two first axes accounted for 43.7 percent (27.7 and 16.0 percent, see Figure 4.3.A) of the variation in species RIV among the sites, while the third one accounted for 9.1 percent of the variation and identified groups were significantly

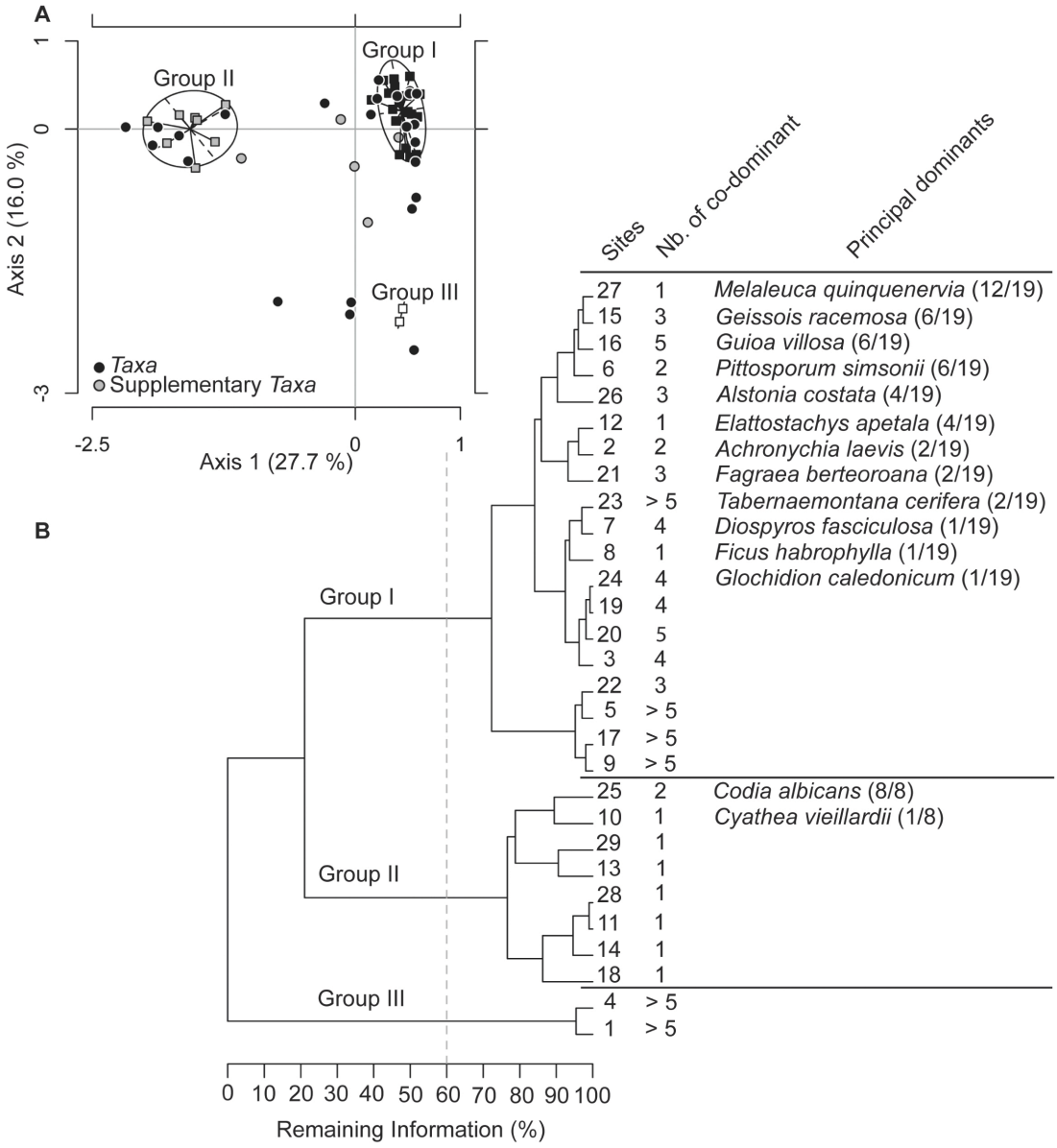


Figure 4.3 *Projection of sites and species on the two first axis of the FCA (A) with 3 identified sites clusters groups (Group I. II and II) identified on the HAC dendrogram (B). For each site, the number of co-dominant species determined by the dominance analysis and for each groups the list of the dominant species (with the number of sites within the cluster groups where the species was dominant against the total number of sites of the cluster group).*

different (ANOSIM R statistic = 1, *i.e.* complete separation between groups, p-value < 0.001) according to their species' RIV composition.

4.5.2 Two different patterns of early secondary successional forest

We identified two different patterns of early secondary successional forest on the first axis of the FCA (Group II and I). The first pattern (Group II) included sites dominated by *Codia albicans* (accounting for 58.3 percent of the total inertia of the first axis of the FCA), where $RIV_{Codia\ albicans}$ was *ca* 80 percent on average (from 71.8 to 88.6 percent) with 0.22 (± 0.07) individuals / m^2 on average, whereas *Codia albicans* was absent from the others sites (Group I and III, Figure 4.3).

Seven among the eight sites corresponding to the first successional pattern (Group II), were only dominated by *Codia albicans* suggesting monodominant formations (see HAC and dominance analysis, Figure 4.3.B). In this first pattern, *Codia albicans* was associated, on the negative part of the first axis of the FCA, to *Styphelia cymbulae*, *Archidendropsis fulgens*, *Gardenia oudiepe*, *Cyathea vieillardii* and *Deplanchea speciosa* (Figure 4.4.A). Among these species, *Gardenia oudiepe* was also inventoried in two sites of the Group I (sites 16 and 26) and *Cyathea vieillardii* and *Deplanchea speciosa* on only one of these two sites (26).

Sites corresponding to the second successional pattern (Group I) were co-dominated by one to more than five species most probably according to the state of the savanna re-colonization. Presumed earlier stages of re-colonization were still dominated by *Melaleuca quinquenervia* the savanna dominant tree (sites 8, 12 and 27, with $RIV_{Melaleuca\ quinquenervia}$ = 65.6, 64.5 and 68.8 percent, respectively), whereas presumed more advanced stages of re-colonization were co-dominated by species such as (sorted by decreasing order of importance): *Geissois racemosa*, *Guioa villosa*, *Pittosporum simsonii*, *Alstonia costata* and *Elattostachys apetala* (Figure 4.3). Thus the species diversity calculated by the Shannon-Weaver diversity index was higher (Wilcoxon test, p-value < 0.01) for this second pattern (Group I, mean H' = 0.83 ± 0.19) than the first one (Group II, mean H' = 0.47 ± 0.22).

Dealing with the occurrence of species specimens in different formation types from herbarium data, two points were worthy to note. Firstly, as *Codia albicans* and

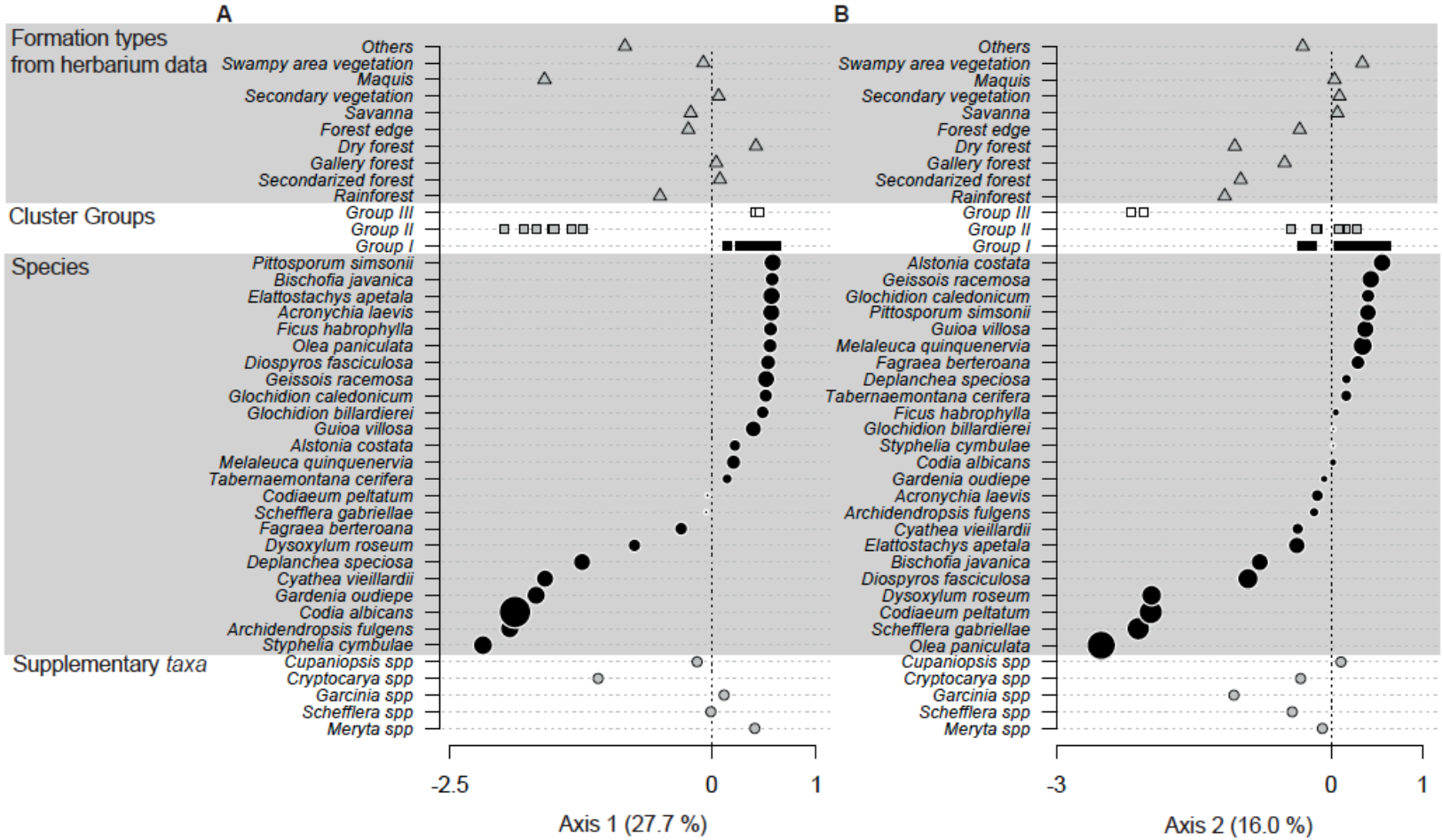


Figure 4.4 *Representation of the formation types from the herbarium data, taxa and the inventory plots on the axis 1 (A) and 2 (B) of the FCA (see* Figure 4.3.A*). Black circles represent species with diameters proportional to the contribution of the species to the building of the axis.*

Styphelia cymbulae were highly collected in maquis (47.4 and 70.6 percent of the collects, respectively, Table 4.3), sites of the Group II were associated to maquis on the first axis of the FCA (Figure 4.4.A). Secondly, among the 19 specimens of *Codia albicans* collected, *ca* 65 and 35 percent were collected in open and closed formations respectively, while none of them were collected in semi-open formations (Figure 4.5) suggesting a rapid closure of the area colonised by *Codia albicans*.

4.5.3 Closure gradient from early to advanced secondary successional forests

The second axis of the FCA that discriminated sites of the Groups I and III and associated species showed a gradient of the canopy closure from open early secondary formation to closed advanced secondary successional forest (Figure 4.4.B). This interpretation of the observed gradient was confirmed by the position of formation types on the axis with open formations (swampy area vegetation, maquis, secondary vegetation and savanna) on the positive part of the axis, semi-open formations (forest edge, dry forest, gallery forest and secondarized forest) on the negative part and closed formation (rainforest) on the most negative part.

This second FCA axis was mainly built by *Olea paniculata*, *Codiaeum peltatum*, *Schefflera gabriellae, Diospyros fasciculosa and Dysoxylum roseum* that accounted for 35.6, 14.0, 11.7, 7.0 and 6.2 percent of the total inertia, respectively. These five species, as the two sites (1 and 4) of the Group III, were positioned on the very negative part of the second axis of the FCA (Figure 4.4.B), characterizing an advanced secondary successional forest. Indeed, at the New Caledonian scale, according to herbarium data, *Olea paniculata* and *Diospyros fasciculosa* on the one hand and *Dysoxylum roseum Schefflera gabriellae and Codiaeum peltatum* on the other hand, were none and poorly collected in open formations, respectively, but more in closed or semi-open formations (Figure 4.5). Conversely, on the positive side of the second FCA axis or closest to zero, the specific cortege that characterized open early secondary succession was dominated by *Geissois racemosa*, *Guioa villosa*, *Pittosporum simsonii*, *Alstonia costata*, *Elattostachys apetala*, *Achronychia laevis*, *Fagraea berteoroana*, *Tabernaemontana cerifera* and *Glochidion caledonicum*. Herbarium specimens of these species were globally more collected in open formations than those of the precedents (Figure 4.5).

However, note that half of the specimens of *Geissois racemosa* and *Alstonia costata* were collected in closed formations (rainforest) suggesting persistence during secondary succession.

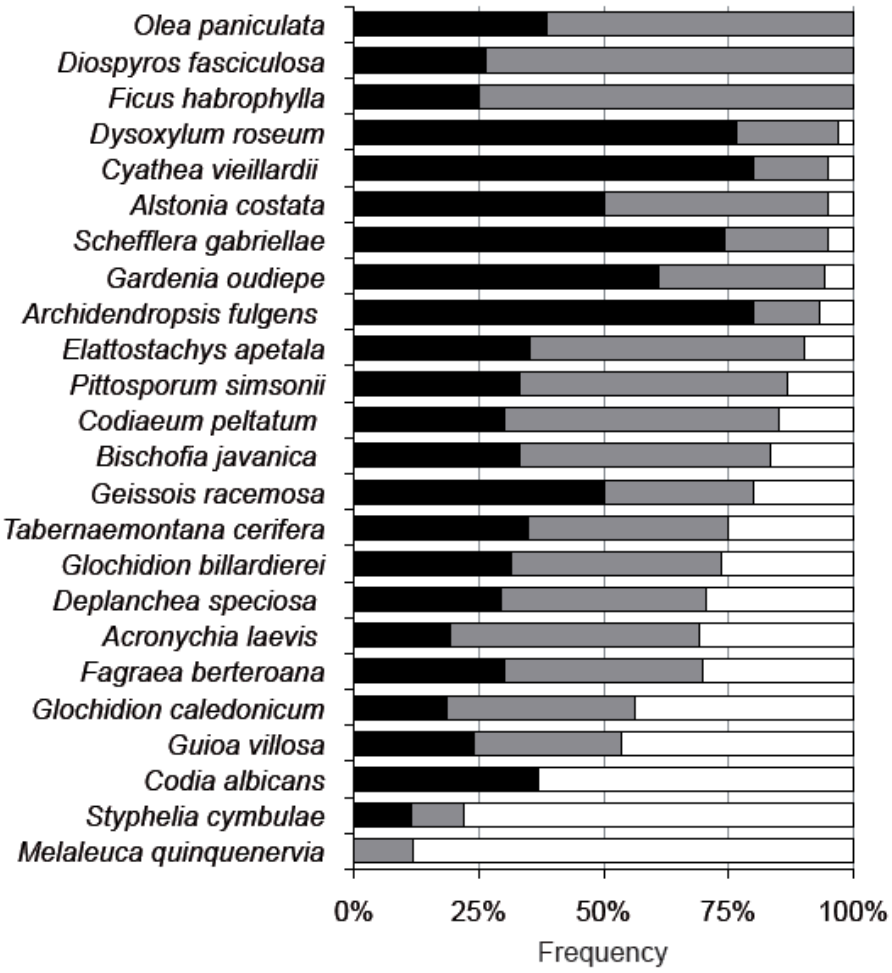


Figure 4.5 *Frequency of collects of species herbarium specimens in open (white), semi-open (grey) and closed ecosystems (black). Species were classified into a decreasing order of frequency into open ecosystems and into an increasing order of frequency into closed ecosystems.*

4.5.4 Species ecology of early secondary successional forest

Field and herbarium data analysis suggested that, among the 24 studied species, 10 species encompassing trees and small trees and accounting for 62.2 percent of the total inventoried trees (71.8 percent without taking into account the savanna dominant tree *Melaleuca quinquenervia*) were most likely to be pioneer species in the savanna to

rainforest secondary succession (Table 4.3). Three of these species are dispersed by wind (*Alstonia costata, Codia albicans* and *Geissois racemosa*) while the others are likely dispersed by birds.

These 10 identified pioneer species were globally ubiquitous species (Figure 4.6) growing in different formations (Figure 4.5) and substrate types and on a wide range of elevations (Table 4.3). Indeed, all these species grow on both acidic and ultramafic rocks, but the half were not collected on calcareous rocks (*Codia albicans*, *Geissois racemosa*, *Guioa villosa, Pittosporum simsonii* and *Tabernaemontana cerifera*) and ranging from 0 - 400 and to 0 - 1100 m asl.

Among these species, two different patterns of population structure were identified in the Figure 4.7: (1) a pattern associated to shade-tolerant species, where both the lower DBH classes showed the higher frequency and with seedlings abundant in the undergrowth (*Codia albicans*, *Acronychia laevis, Elattostachys apetala*, *Guioa villosa, Tabernaemontana cerifera* and *Fagraea berteroana*) and (2) a pattern associated to shade-intolerant species, where fewer trees were present in the lower DBH classes and few or no seedlings in the undergrowth (*Geissois racemosa*, *Alstonia costata* and *Pittosporum simsonii*). None *Geissois racemosa* seedlings were inventoried suggesting that this species cannot regenerate in the undergrowth.

Table 4.3 *Ecology of identified main pioneer species. Herbarium specimens distributions on different edaphic units were issued from the simplification of* (Fritsch 2011).

Species	Type	Dispersal syndrome	N	Edaphic units					Elvation range (m asl)
				Acidic (%)	Ultramafic (%)	Calcareous (%)	Wetlands (%)	NA (%)	
Achroychia laevis	Little tree	Bird	113	36 (31.9)	36 (31.9)	7 (6.2)	13 (11.5)	21 (18.6)	0 - 850 m
Alstonia costata	Tree	Wind	103	35 (34.0)	27 (26.2)	1 (1.0)	15 (14.6)	25 (24.3)	0 - 900 m
Codia albicans	Tree	Wind	32	10 (31.3)	17 (53.1)	0 (0.0)	1 (3.1)	4 (12.5)	0 - 1080 m
Elattostachys apetala	Tree	Bird	94	40 (42.6)	31 (33.0)	12 (12.8)	7 (7.4)	4 (4.3)	0 - 900 m
Fagraea berteroana	Litlle tree	Bird	22	12 (54.5)	6 (27.3)	3 (13.6)	1 (4.5)	0 (0.0)	0 - 600 m
Geissois racemosa	Tree	Wind	30	23 (76.7)	5 (16.7)	0 (0.0)	0 (0.0)	2 (6.7)	0 - 500 m
Glochidion spp.[a]	Litlle tree	Bird	210	62 (29.5)	33 (15.7)	35 (16.7)	13 (6.2)	67 (31.9)	0 - 700 m
Guia villosa	Little tree	Bird	225	34 (15.1)	79 (35.1)	0 (0.0)	9 (4.0)	103 (45.8)	0 - 1100 m
Pittosporum simsonii	Tree	Bird	97	42 (43.3)	23 (23.7)	0 (0.0)	9 (9.3)	23 (23.7)	0 - 400 m
Tabernaemontana cerifera	Little tree	Bird	185	60 (32.4)	76 (41.1)	0 (0.0)	4 (2.2)	45 (24.3)	0 - 550 m
Total	-	-	1111	354 (31.9)	333 (30.0)	58 (5.2)	72 (6.5)	294 (26.5)	-

[a]Encompassing *Glochidion biellarderi* and *Glochidion caledonicum*

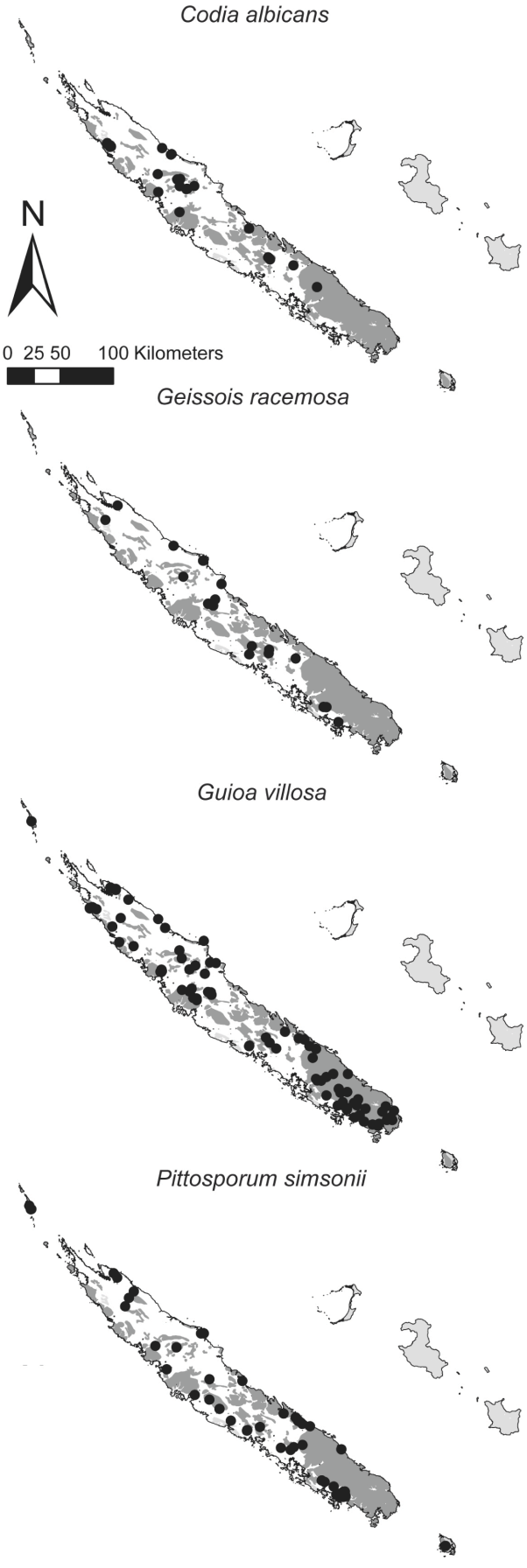


Figure 4.6 *Specimens' distribution of four of the main identified pioneer species. The base map is a simplification from* (Fritsch 2011) *showing calcareous substrate (light grey), ultramafic substrate encompassing peridotite and serpentinite (dark grey) and acidic substrate (white).*

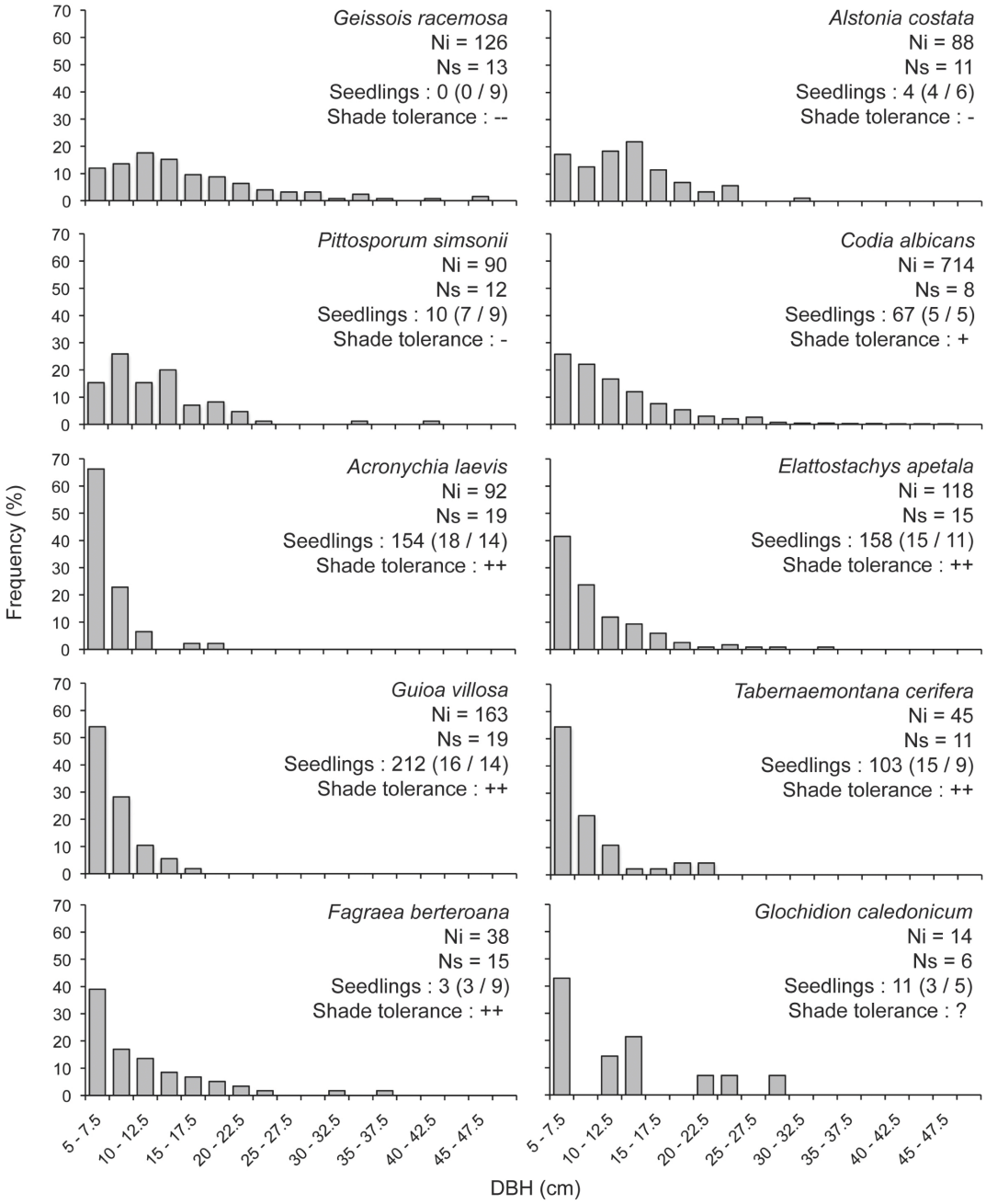


Figure 4.7 *Population structure of the 10 most likely pioneer species. Ni stands for number of individuals, Ns for the number of sites where the species was sampled, and seedlings for the total number of seedlings indentified with the ratio of the number of sites where seedlings were identified against the number of sites where both trees were sampled and seedlings inventory was performed. Four class of shade tolerance were hypothesised according to the structure of the population and the seedlings inventory: very shade-intolerant (--), shade-intolerant (-), shade-tolerant (+), very shade-tolerant (++).*

4.6 Discussion

4.6.1 Mono-dominant *Codia albicans* formation

Our results highlighted eight sites (Group II) dominated by *Codia albicans* that can be qualified as mono-dominant formation (Connell and Lowman 1989). Such mono-dominant formations are not rare across the tropics (Connell and Lowman 1989; Hart *et al.* 1989; Torti *et al.* 2001). In the studied landscape, these mono-dominant *Codia albicans* formations occurred preferentially on ridges and at the interface of savanna and mixed rainforest. How to explain the presence of these *Codia albicans* mono-dominant formations?

Connell & Lowman (1989) proposed an array of mechanisms that could produce mono-dominated formation. Given that *Codia albicans* juveniles were abundant in the undergrowth, *Codia albicans* likely persists beyond one generation. Thus, *Codia albicans* mono-dominant formations can be qualified, according to Connell & Lowman (1989), as a Type-I mono-dominant formation (*i.e.* "*with a persistent dominant*"). In our case, the presence of such Type-I mono-dominant formation may be linked to the fact that *Codia albicans*, being a wind-dispersed species (Pillon *et al.* 2009), is likely to be the most common species first colonising an area opened by fire or cyclone. However, we cannot conclude here if the dominance of *Codia albicans* juveniles in the undergrowth, which allows them to persist beyond one generation is only due (1) to higher seed sources than other local tree species, and / or (2) to the fact that *Codia albicans* is better adapted to local environmental condition (*e.g.* soil characteristics) than all other local tree species (Connell and Lowman 1989).

Read *et al.* (1995) described another mono-dominant forest type in New Caledonia on ultramafic substrates dominated by the *Nothofagus* genus. We suggest that as for the *Nothofagus* spp. mono-dominant forests, *Codia albicans* mono-dominant formations are an early successional stage following disturbance such as fire (*e.g.* at the rainforest-savanna edge) or cyclone (*e.g.* on the wind exposed ridge), and are potentially replaced by mixed rainforest species in the absence of further disturbances (Chatain *et al.* 2009; Read *et al.* 1995; Read *et al.* 2006). The hypothesis of post-fire succession is in our case reinforced by (1) the presence of few old growth *Melaleuca quinquenervia*,

a bio-indicator of the presence of savanna favoured by fire before the arrival of *Codia albicans*, and (2) the presence of rainforest trees such as *Archidendropsis fulgens*, *Cryptocarya* spp., *Schefflera* (*Plerandra*) spp. and *Dysoxylum* spp., indicating that *Codia albicans* mono-dominant forests will likely be slowly replaced by mixed rainforest species.

At the New Caledonian scale*, Codia* is an endemic genus that encompasses 14 species (Hopkins *et al.* 2007). Substrate type is likely to be one of the main drivers of *Codia* distribution, as most *Codia* species preferentially grow on ultramafic substrates, while some species likes *Codia albicans* growth on both ultramafic and non-ultramafic substrates (Pillon *et al.* 2009). As for *Codia albicans*, other *Codia* mono-dominant formations were observed in New Caledonia on acidic rocks, *e.g. Codia mackeeana* (at the *Parc des grandes fougères*, pers. obs.) and *Codia incrassata* (at *Tendo*, pers. obs.). The presence of these different *Codia* spp. mono-dominant formations suggests a peculiar ecology of this genus developed below for *Codia albicans*.

4.6.2 Different patterns of successional forests

The second successional pattern was co-dominated by a mix of species, however our results highlighted the importance of *Geissois racemosa*. The comparison of early secondary successional forests dominated by *Codia albicans* or co-dominated by *Geissois racemosa* that also belongs to Cunoniaceae (Hopkins 2006), suggests two different colonization strategies for open areas that lead to different secondary succession types. Early secondary successional forests co-dominated by *Geissois racemosa* showed a more diversified and complex species composition, and were also often dominated or co-dominated at least by wind dispersed pioneer species: *Geissois racemosa* and *Alstonia costata*.

In contrast to *Codia albicans, Geissois racemosa* is likely to be shade intolerant (since no juveniles were observed in the undergrowth even when *Geissois racemosa* co-dominated the canopy). Thus *Geissois racemosa* and *Codia albicans* most likely colonize open areas first. However, *Codia albicans'* colonization leads to dense mono-dominated colonization front lines, while *Geissois racemosa* leads to open colonization associated to other wind- (*Alstonia costata*) or bird- (such as *Guioa villosa*, *Pittosporum*

simsonii or *Acronychia laevis*) dispersed pioneer species. This difference in colonization patterns may be due to difference in dispersal patterns (Franklin and Rey 2007; Seidler and Plotkin 2006). The main plant attributes acting on dispersal pattern of seeds by wind are the aerodynamic proprieties of diaspores and the height from which they are released (Greene and Johnson 1989; Nathan *et al.* 2001). We suggest that tree and diaspore morphological differences between *Geissois racemosa* (winged seeds in dehiscent fruit) and *Codia albicans* (woolly seeds and fruit with indehiscent fruit) may explain, at least partially, differences observed in the patterns of successional forests. Indeed, *Geissois racemosa* trees are taller, and acquire their fecundity later than *Codia albicans*, this probably due to a longer life time for *Geissois racemosa* (unpublished data). Given that *Geissois racemosa*'s seeds are likely to be released from a greater height and thus to disperse further away from the parent tree than *Codia albicans* (Tackenberg *et al.* 2003), this may lead to sparser formations.

Although *Geissois racemosa* is a shade-intolerant species, it was collected in both open and closed ecosystems. Indeed, *Geissois racemosa* was widely observed as isolated trees in savannas and as canopy dominant tree (in terms of height) in rainforests, suggesting that *Geissois racemosa* is a long-lived tree growing in open ecosystems (such as savanna) and persisting during the successional process by standing above the crowns of the others trees species. In both cases, these trees may play an important role in the secondary succession: (1) isolated trees in savannas potentially increase birds' and bats' (attractive flowering for flying-foxes) dispersed seed arrivals by promoting a perch-effect (Guevara *et al.* 1986; Holl *et al.* 2000; McDonnell and Stiles 1983) and nucleation processes (Reis *et al.* 2010), and (2) tall rainforest canopy dominant trees by produce seeds that may be dispersed by wind into savannas.

4.6.3 Advantages and limits of using herbarium data

Herbariums are great sources of ecological data, encompassing localisations of specimens and associated environmental data collected by experienced taxonomists and regularly checked by specialists. This paper shows how herbarium environmental data such as ecosystems types, soils types and elevation may be used to complete and

validate field observations at a broader spatial scale. However, as Garcillan & Ezcurra (2011) and Crawford & Hoagland (2009), we noted several biases in our herbarium dataset linked to the collect of the specimens and associated environmental data.

Firstly, as one would expect, the sampling effort is not homogeneous in respect to the different ecosystems and their localisation. Indeed, although we worked on rainforest-savanna dynamic, less than two percent of the specimens of our species of interest were collected in savanna, while *ca* 20 percent were collected in maquis. This bias may be due to the fact that collectors tend to collect more in rich and diverse ecosystems such as rainforest or maquis (Jaffré *et al.* 2009) than in poor degraded ones such as savanna and other secondary vegetations types. Moreover collectors tend to focus their sampling efforts towards rare species, often paradoxically failing to collect the most common ones (Garcillan and Ezcurra 2011).

Secondly, the additional ecological informations are not always mentioned and suffer from a lack of homogeneity in terminology (*i.e.* among the 708 specimens of our dataset we counted 296 different terminologies for the description of the formations and we finally found a consensus in the formations classification with 10 types presented here).

4.6.4 Implication for restoration

Using field sampling associated to herbarium data analysis, we identified 10 species (Table 3) as main pioneer species and potential candidates for forest restoration. These species were mainly ubiquitous species, growing on a wide range of substrate types and elevations, suggesting that they may be used for restoration in the different New Caledonian degraded habitats. However as field sampling was done in a restricted area (the western side of the *Aoupinié* mountain), field surveys in different New Caledonian localities would be critical to complete this list. As an example, we noted that early secondary formation dominated by *Codia albicans* on the *Aoupinié* may be dominated by other *Codia* species in others localities (*e.g. Codia incrassata*, *Codia mackeeana*). Moreover, others *taxa* not identified at the species level such as *Cupaniopsis* spp. inventoried in 12 among the 29 sites may be also potential target species for restoration.

Understanding the different patterns of secondary succession is critical to choose the species to plant according to the objective of the restoration. For instance, our results suggest that planting *Codia albicans* may lead to a rapid closure of the canopy but a slow biodiversity recovery, while planting *Geissois racemosa* may lead to a slower closure of the canopy but a faster biodiversity recovery as it is not competing with other species in the undergrowth.

Seed dispersal limitation is one of the main barriers to forest recovery in degraded area in the tropics such as savannas in New-Caledonia (e.g. Aide and Cavelier 1994; Hooper *et al.* 2005). This barrier may be overcome by planting tree to structure the degraded area and enhance the natural seed arrivals (Holl *et al.* 2000). We suggest that planting *Geissois racemosa* associated to a mix of bird dispersed species such as *Guioa villosa* and *Pittosporum simsonii* to enhance bird and flying-foxes attraction and facilitate forest regeneration under their canopies may be a good way to accelerate forest secondary succession in New Caledonian savannas. However, others barriers have to be overcome. Indeed, in the studied area but also in many places in New Caledonia and others countries in the tropics, perturbations such as recurrent bush fires, grazing by introduced ungulates, and competition with weeds such as *Lantana camara*, *Mimosa diplotricha* or *Melinis minutiflora* slow down or prevent any secondary succession. Thus removing or reducing these barriers is critical to maximise the restoration effort and the forest recovering.

4.7 Acknowledgments

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4.8 Appendix

Inventoried *taxa* identified at genus or species levels

Family	Species name	Status[a]
Anacardiaceae	*Semecarpus atra* (Forster) Vieill.	E
Annonaceae	*Meiogyne* spp.	E
	Polyaltrhia nitidissima (Dunal) Benth.	A
Apocynaceae	*Alstonia costata* (G. Forster) R. Brown	E
	Alstonia lanceolata (Van Heurck)	
	Tabernaemontana cerifera Pancher & Sebert	E
Aquifoliaceae	*Ilex sebertii* Pancher & Sebert	E
Araliaceae	*Meryta* spp.	-
	Schefflera gabriellae Baill.	E
	Schefflera spp.	-
	Tieghemopanax spp.	-
Bignoniaceae	*Deplanchea speciosa* Vieill.	E
Bischofiaceae	*Bischofia javanica* Blume	A
Chrysobalanaceae	*Hunga rhamnoides* (Guillaumin) Prance	E
Cunoniaceae	*Codia albicans* Vieill.	EE
	Geissois racemosa Labill.	E
	Pancheria ternata Brongn.	EE
Cyatheaceae	*Cyathea veillardii*	A

Dilleniaceae	*Tetracera billarderi* Martelli	E
Ebenaceae	*Diospyros fasciculosa* (F. Muell.) F. Muell.	A
Elaeocarpaceae	*Elaeocarpus angustifolius* Blume	A
Epacridaceae	*Styphelia cymbulae* (Labill.) Sprengel	A
Euphorbiaceae	*Aleurites moluccana* (L.) Wild.	A
	Bocquillonia spp.	EE
	Claoxylon insulanum Muell. Arg.	E
	Cleidion spathulatum Baill.	E
	Codiaeum peltatum (Labill.) P.S. Green	A
	Glochidion billardieri Baill.	E
	Glochidion caledonicum Muell. Arg.	E
	Glochidion spp.	E
	Macaranga coriacea (Baill.) Muell. Arg.	E
Flacourtiaceae	*Homalium* spp.	E
Gutiferae	*Garcinia* spp.	E
Labiatae	*Oxera robusta* Vieill	E
Lauraceae	*Cryptocarya* spp.	-
Lectythidiaceae	*Barringtonia longifolia* Schltr.	E
Linaceae	*Hugonia* spp.	-
Loganiaceae	*Fagraea berteroana* A.Gray.	A

	Geniostoma vestitum Baill.	-
Meliaceae	*Dysoxylum bijugum* (Labill.) Seeman	A
	Dysoxylum kouiriense Virot	E
	Dysoxylum roseum C. DC.	E
	Dysoxylum spp.	-
Mimosaceae	*Alblisia Lebeek* Durazz.	I
	Archidendropsis fulgens (Labill.) Nielsen	E
	Archidendropsis granulosa (Labill.) Nielsen	E
	Archidendropsis spp.	E
Monimiaceae	*Hedycarya* spp.	E
Moraceae	*Ficus fraseri* Miq	A
	Ficus habrophylla Bennett ex Seemann	A
	Ficus spp.	-
Myrsinaceae	*Rapanea* spp.	-
	Rapanea asymmetrica Mez	E
	Tapeinosperma spp.	-
Myrtaceae	*Carpolepis laurifolia* J.W. Dawson	EE
	Melaleuca quinquenervia (Cav.) S.T. Blake	A
	Piliocalyx spp.	E
	Psidium guajava L.	I
Oleaceae	*Chionanthus brachystachys* (Schltr.) P.S. Green	A
	Olea paniculata R.Br.	A
Piperaceae	*Piper austrocaledonicum* C.DC.	A

Proteaceae	*Kermadecia sinuata* Brongn. & Gris	EE
Pittospraceae	*Pittosporum simsonii* Montrouz.	E
Rhizophoraceae	*Crossostylis grandiflora* Pancher ex Brongn. & Gris	E
Rubiaceae	*Gardenia oudiepe* Vieill.	E
	Psychotria douarrei (Beauvis.) com. Ined	E
	Psychotria schlechteriana Krause	E
Rutaceae	*Acronychia laevis* Forster & G.Forster	A
	Sarcomelicope leiocarpa (P.S. Green) T. Hartley	E
Sapindaceae	*Cupaniopsis* spp.	-
	Cupaniopsis glomeriflora Radlk.	E
	Elattostachys apetala (Labill.) Radlk.	A
	Guioa villosa Radlk.	E
Symplocaceae	*Symplocos arborea* (Vieill.) Brongn. & Gris	E
Thymelaeceae	*Lethedon* spp.	E
Urticaceae	*Pipturus argenteus* (Forster) Wedd.	A

[a] EE for endemic genus, E for endemic species, A for authoctonous species, I for introduced species.

5 Structures and patterns of New Caledonian secondary forest

This section presents preliminary results as supplementary material, which will not be submitted for publication.

5.1 Introduction

Spatial analyses allow plant ecologists to highlight the underlying processes (*e.g.* dispersal limitation, environmental heterogeneity, competition and density- or distance dependant mortality) that produce an observed pattern. We used point pattern analyses using the R packages *ads* (Pelissier and Goreaud 2009) and *spatstat* (Baddeley and Turner 2005), with personal functions to analyze the intra- and inter-species relationships. We intended to decipher spatial processes involved during the secondary succession from savanna to rainforest.

5.1.1 State of the art in point pattern analysis in forest ecology

A point pattern dataset gives the location of objects (*e.g.* trees) or events represented by points attributes in a study area (*e.g.* forest stand). Each object may be characterised by additional information called *marks*, which can be categorical (*e.g.* species, dispersal syndrome), continuous (*e.g.* tree diameter, tree height) or multivariate (see Illian *et al.* 2008).

The aim of point pattern analysis is to characterise locations of such objects (points), for one class of objects, *e.g.* whether they are clustered, randomly or regularity distributed or for two classes of objects (*e.g.* two different tree species), whether there is repulsion, attraction or total independence (random inter-distribution) between the classes. In forest ecology, such distributions may be linked to different pattern of seed dispersal or to other ecological processes such as intra or inter-specific competition, facilitation or disturbance (e.g. Bossdorf *et al.* 2000; Condit *et al.* 2000; Pelissier 1998; Stoyan and Penttinen 2000; Wiegand *et al.* 2009).

Numerous methods for the analysis of point pattern data have been developed (Cressie 1991; Diggle 2003; Illian *et al.* 2008; Law *et al.* 2009; Perry *et al.* 2006; Perry *et al.* 2002; Stoyan and Penttinen 2000; Wiegand and Moloney 2004). These different methods encompass first-order statistics, which describes large-scale variations such as intensity (λ, *i.e.* expected number of points per unit of area). Second-order statistics, which are summary statistics of all point-to-point distances in a point pattern dataset,

are also concerned. First- and second-order statistics may be used to characterize point patterns under the assumptions of stationnarity (or homogeneity) and isotropy (*i.e.* invariance by rotation and translation).

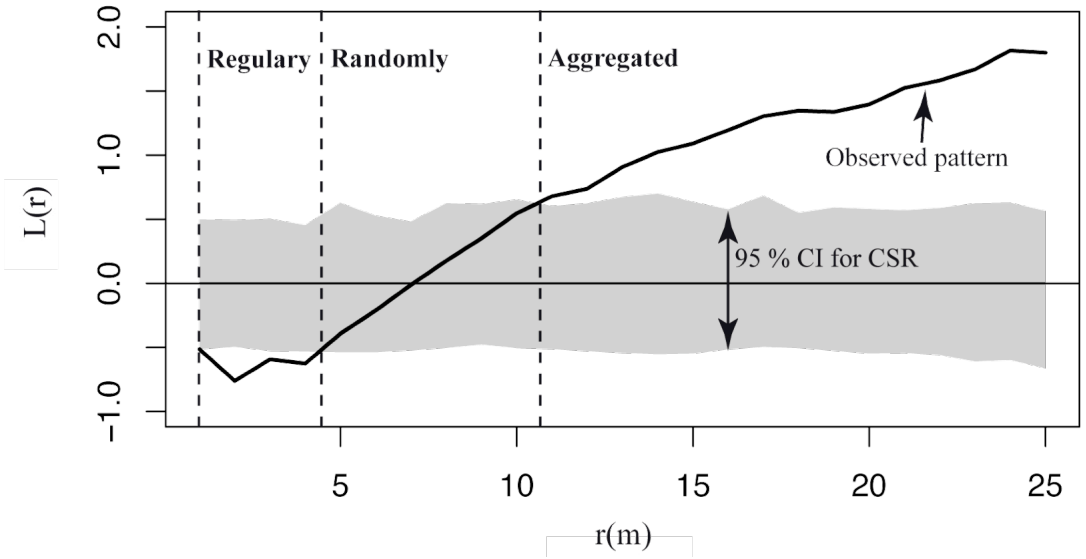

Figure 5.1 *Example of interpretation of estimated L-function (from the BPoirier dataset, ads R package). Black solid lines show the estimated L for different distance (r) and grey areas represent the 95 % CI for CSR (500 simulations). The observed spatial pattern significantly differs from CSR when the black solid line is outside the grey area. When the black solid line is under the grey area (and under 0) the points are regularly distributed (repulsion between points) and when the black solid line is above the grey area (and above 0) the points are aggregated (attraction between points).*

Among the second-order summary statistics, the most popular are the nearest neighbour distribution function (*G*), the Ripley's *K* function (Ripley 1976) and the *L* function (Figure 5.1), which is a linearization of the *K* function (Besag 1977):

$$\hat{\lambda} = \frac{N}{A}$$

$$\hat{G}(r) = 1 - \exp^{(-\hat{\lambda} \times \pi \times r^2)}$$

$$\hat{K}(r) = \frac{1}{\hat{\lambda}} \times \frac{1}{N} \sum_{j=1}^{N} \sum_{j \neq i} k_{ij}$$

$$\hat{L}(r) = \sqrt{\frac{\hat{K}(r)}{\pi}} - r$$

where N is the number of objects in the studied area, A is the area, r is the distance, k_{ij} = 1 if the distance between the points i and j is ≤ r and k_{ij} = 0 if this distance is > r (Goreaud and Pelissier 1999). The spatial relationship between two types of points (*e.g.* two tree species of number N1 and N2) may be characterised using the intertype K_{12}-function, which is an extension of the Ripley's *K*-function.

$$\hat{K}_{12}(r) = \frac{1}{\hat{\lambda}_2} \times \frac{1}{N_1} \times \sum_{i=1}^{N_1} \sum_{j=1}^{N_2} k_{12} \text{ with } \hat{\lambda}_2 = \frac{N_2}{A}$$

$$\hat{L}_{12} = \sqrt{\frac{\hat{K}_{12}}{\pi}} - r$$

where k_{ij} = 1 if the distance between the points i of type 1 and j of type 2 is ≤ r and k_{ij} = 0 if this distance is > r (Goreaud and Pelissier 2003). Some methods have been developed to work with non-stationnarity (heterogeneity) however the estimators of these second-order summary statistics are pretty more complex (Couteron *et al.* 2003). An alternative solution is to split the heterogeneous area into several homogeneous areas and to analyse them separately (Pelissier and Goreaud 2001).

The second-order characteristics based on point-to-point distances require edge correction as the number of neighbours at distance r can be underestimated for the points located near edges of the studied area. Some of these neighbours are likely located outside the study area (Goreaud and Pelissier 1999; Perry *et al.* 2006). Several methods of edge correction have been developed such as the used of buffer zone and the toroidal duplication of the study area (Haase 1995; Perry *et al.* 2006). However, the most commonly used function is the Ripley's correction, which allows robust and

unbiased estimation of $K(r)$ without drastically reducing the data set (Goreaud and Pelissier 1999).

In order to characterise the observed point pattern (*e.g.* clustered, randomly or regularity distributed), the statistics estimated for the observed point pattern are compared to statistics estimated for point patterns with the same intensity (λ) but with a complete spatial randomness (CSR) simulated using a Poisson process (Perry *et al.* 2006; Stoyan and Penttinen 2000; Wiegand and Moloney 2004).

5.2 Materials and methods

We mapped all trees (diameter at breast height, DBH > 5 cm) of five secondary forest sites from 400 m^2 to 2400 m^2 (see Table 5.1), using an ultrasonic hypsometer (Vertex IV) with 0.1 m uncertainity. However, our analyses focused only on the 2 largest sites (sites 1 and 2, see Figure 5.2 and Figure 5.3) as the others (sites 3, 4 and 5, see Figure 5.4) were to small and did not contained enough trees to perform robust and unbiased analyses of their point pattern. Indeed, it was very difficult to find large and homogeneous secondary forest sites to perform point pattern analysis.

Table 5.1 *General description of the 5 point patterns dataset*

Sites	Dim. (m)	Area (m^2)	Tree			Principal species (% of stems)
			Nb. of stems	Density (stems.ha^{-1})	BA (m^2.ha^{-1})	
1	**40*60**	**2400**	**460**	**1916**	**35.13**	***Melaleuca quinquenervia* (46.3 %)**
						***Alstonia costata* (17.4 %)**
						***Geïssois racemosa* (6.5 %)**
						***Guioa villosa* (5.6 %)**
						***Cupaniopsis spp.* (5.3 %)**
2	**30*30**	**900**	**445**	**4944**	**48.02**	***Codia albicans* (79.9 %)**
						***Fagraea berteoroana* (5.3 %)**
						***Styphelia cymbulae* (3.8 %)**
						***Deplanchea speciosa* (3.4 %)**
3	20*20	400	97	2425	20.47	*Guioa villosa* (43.3 %)
						Pittosporum simsonii (41.2 %)
4	20*20	400	130	3250	43.92	*Codia albicans* (76.9 %)
5	20*20	400	139	3475	61.15	*Codia albicans* (65.2 %)
						Cupaniopsis spp (10.9 %)
Total		3300	905	2824	39.50	

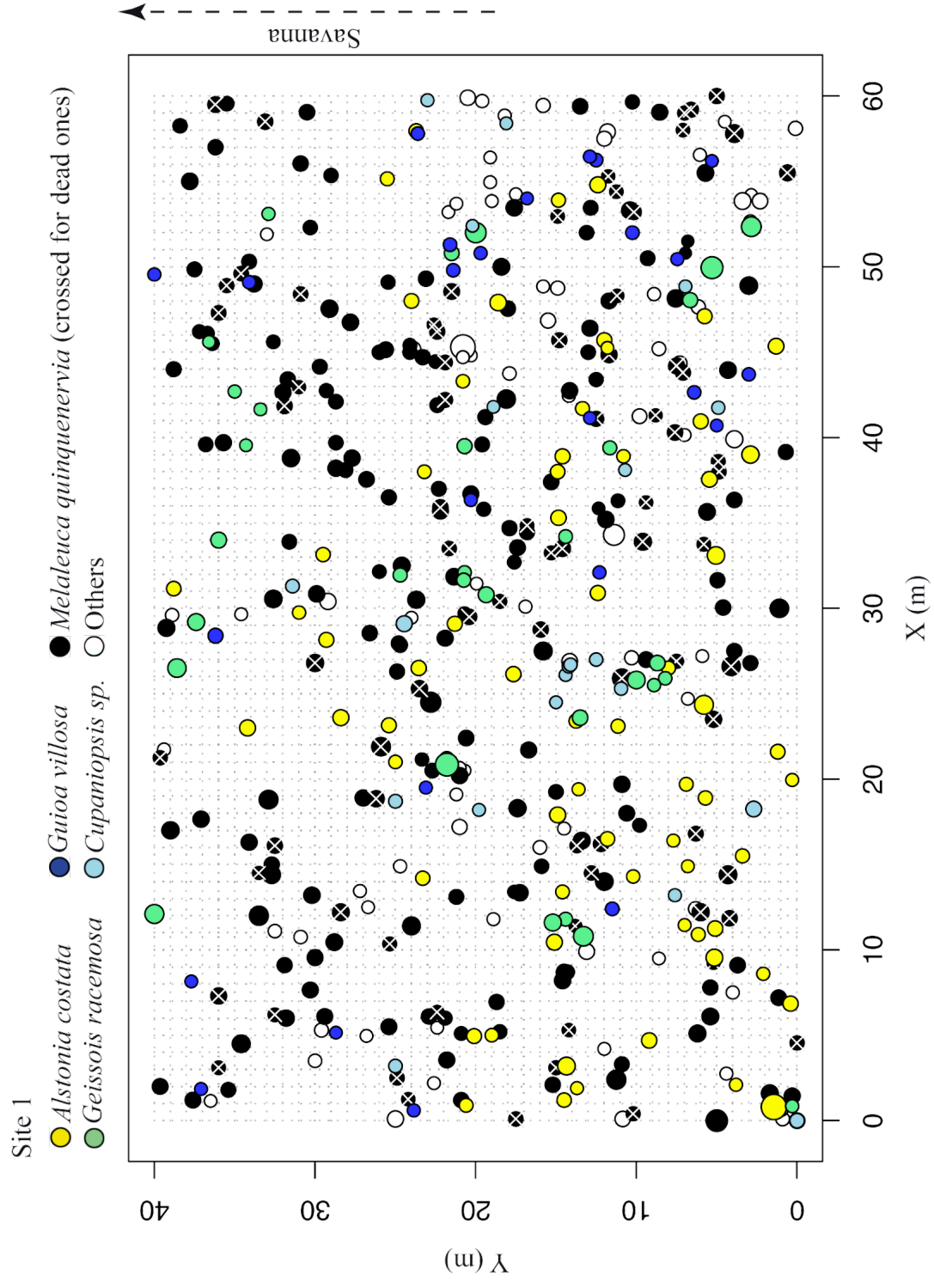

Figure 5.2 *Point pattern site 1 (circles are proportional to the DBH of the trees).*

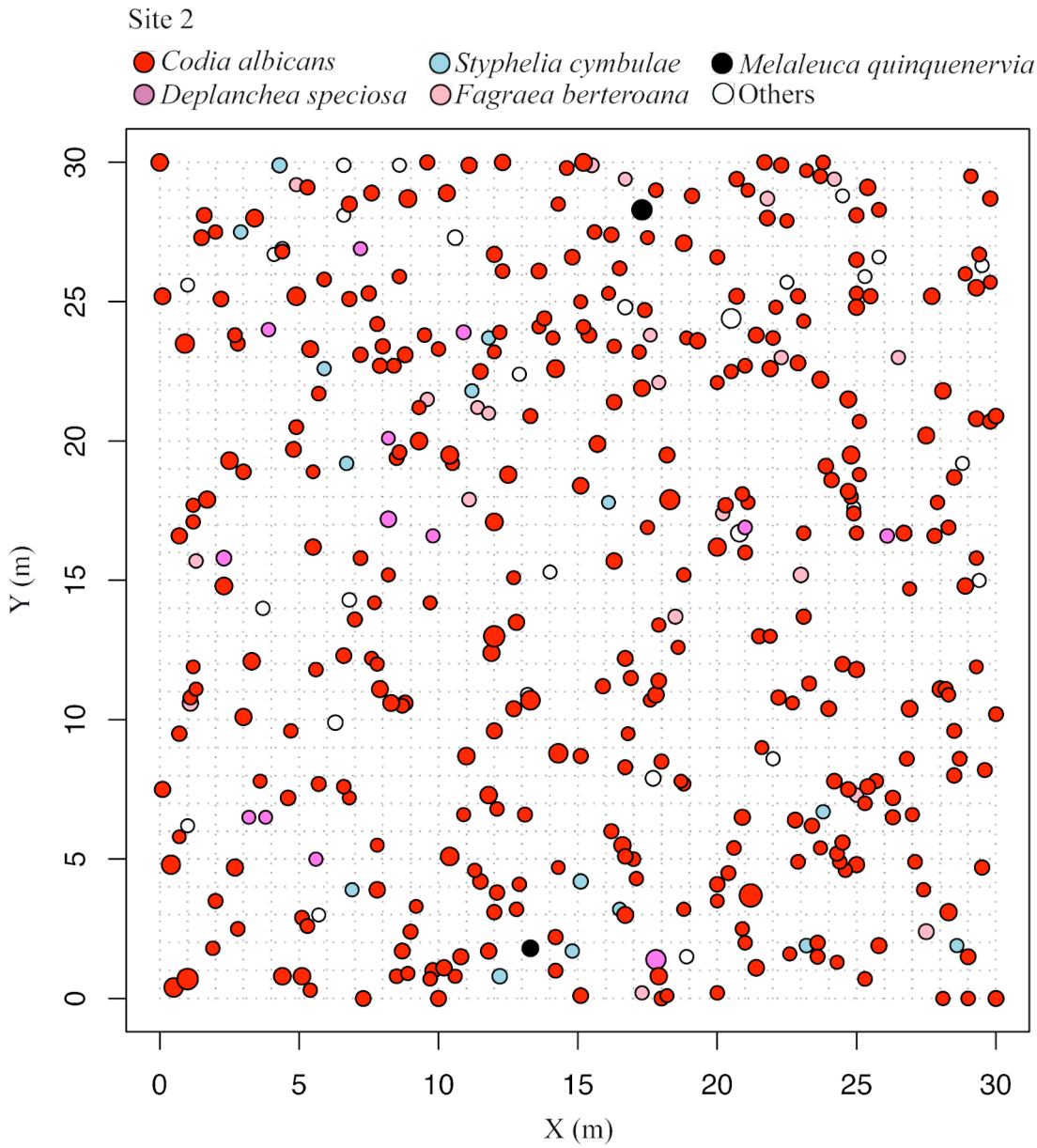

Figure 5.3 *Point pattern site 2 (circles are proportional to the DBH of the trees).*

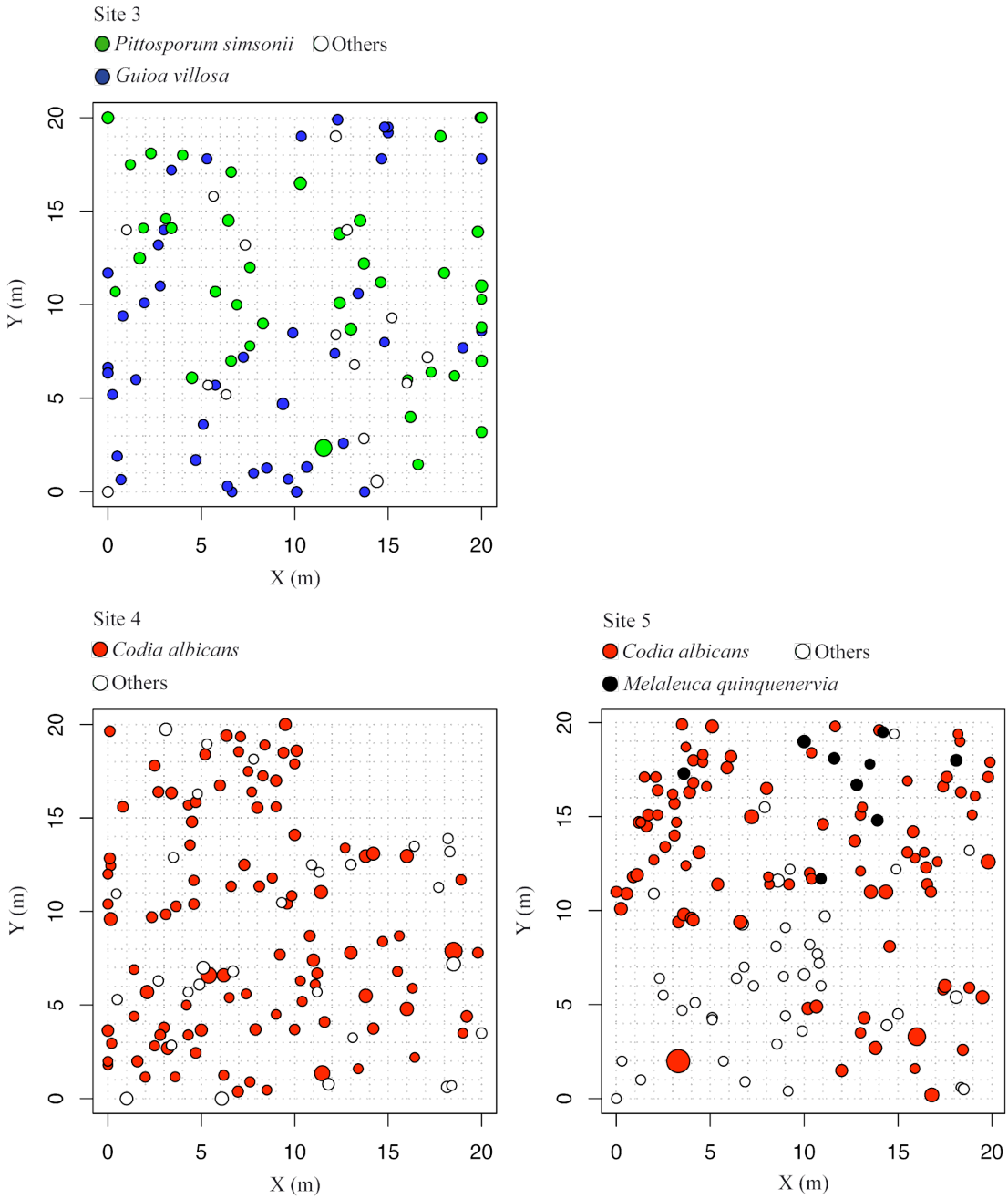

Figure 5.4 *Supplementary point patterns (site 3-5) (circles are proportional to the DBH of the trees).*

Table 5.2 *Species composition of the two studied point patterns (BA for basal area, NI for not identified).*

Sites	Species	Nb. Of stems (%)				Alive stems			Disperal		
		Alive		Dead		DBH (cm)	BA (m^2, %)		Wind	Birds	Others
1	*Melaleuca quinquenervia*	161	(42.5)	77	(95.1)	16.07	3.67	(51.7	X		
	Alstonia costata	64	(16.9)	3	(3.7)	13.85	1.24	(17.4)	X		
	Geissois racemosa	31	(8.2)	-	-	17.48	1.05	(14.8)	X		
	Guioa villosa	25	(6.6)	-	-	7.15	0.11	(1.5)		X	
	Cupaniopsis spp.	21	(5.5)	-	-	8.20	0.13	(1.9)		X	
	Fagraea berteroana	10	(2.6)	-	-	17.27	0.41	(5.8)		X	
	Pittosporum simsonii	10	(2.6)	-	-	11.70	0.13	(1.8)		X	
	Schefflera spp.	10	(2.6)	-	-	13.28	0.16	(2.3)		X	
	Elattostachys apetala	8	(2.1)	-	-	6.61	0.02	(0.2)	X		X
	Merita spp.	8	(2.1)	-	-	5.66	0.02	(0.3)		X	
	Acronychia laevis	4	(1.1)	-	-	5.13	0.01	(0.1)		X	
	Deplanchea speciosa	4	(1.1)	-	-	9.55	0.03	(0.4)	X		
	Ficus habrophylla	4	(1.1)	-	-	7.50	0.02	(0.3)		X	
	Schefflera gabriellae	4	(1.1)	-	-	10.65	0.05	(0.6)		X	
	Ficus sp.	2	(0.5)	-	-	5.15	0.01	(0.1)		X	
	Garcinia sp.	2	(0.5)	-	-	5.75	0.01	(0.1)		X	
	Gardenia oudiepe	2	(0.5)	-	-	8.25	0.01	(0.2)		X	
	Geniostoma vestitum	2	(0.5)	-	-	6.25	0.01	(0.1)		X	
	Glochidion spp	2	(0.5)	-	-	5.80	0.01	(0.1)		X	
	Codia albicans	1	(0.3)	-	-	-	0.02	(0.2)	X		
	Dysoxylum sp.	1	(0.3)	-	-	-	-	-		X	
	Ilex sebertii	1	(0.3)	-	-	-	-	-		X	
	NI	1	(0.3)	-	-	-	-	-	-	-	-

	Symplocos sp.	1	(0.3)	-	-	-	0.01	(0.1)		X		
	Cyathea vieillardii	0	(0.0)	1	(1.2)	-	-	-	X			
Total		379	(100.0)	81	(100.0)	-	7.09	100.0)	-	-	-	
2	*Codia albicans*	322	(84.3)	39	(90.7)	11.02	3.75	(90.1)	X			
	Fagraea berteroana	21	(5.5)	1	(2.3)	7.55	0.10	(2.5)		X		
	Styphelia cymbulae	15	(3.9)	-	-	7.24	0.07	(1.6)		X		
	Deplanchea speciosa	13	(3.4)	-	-	9.22	0.13	(3.0)	X			
	Gardenia oudiepe	7	(1.8)	-	-	5.27	0.02	(0.4)		X		
	Melaleuca quinquenervia	2	(0.5)	2	(4.7)	22.65	0.09	(2.1)	X			
	Schefflera sp.	2	(0.5)	-	-	7.90	0.01	(0.3)		X		
	Alstonia costata	-	-	1	(2.3)	-	-	-	X			
	NI	20	(5.2)	-	-	8.85	0.17	(4.0)	-	-	-	
Total		382	(100.0)	43	(100.0)	-	4.16	(100.0)	-	-	-	

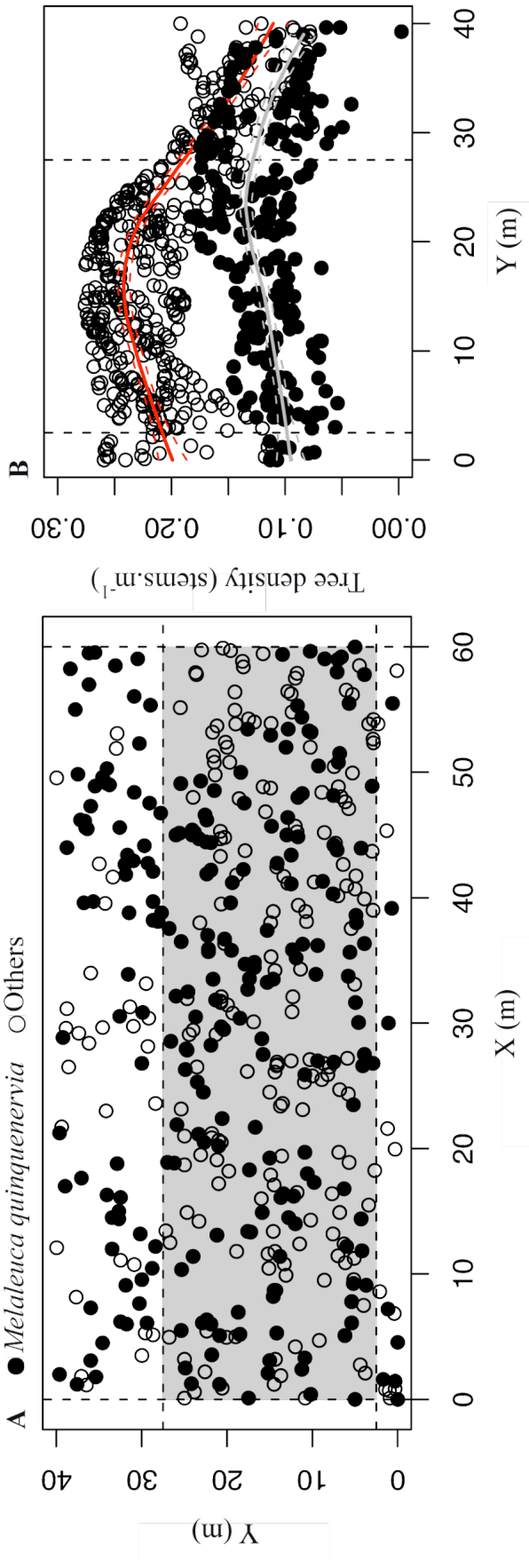

Figure 5.5 *Tree density gradient with A, map of the trees (the grey area represents the homogenous secondary forest delimited on the field) and B, tree density (white circles for all trees and black ones for only Melaleuca quinquenervia) as a function of the Y axis. Dashed lines limit the homogenous secondary forest delimited on the field.*

The two analyzed sites corresponded to two different successional pattern highlighted in Ibanez *et al.* (submitted-c). The first site was co-dominated by the savanna dominant tree species (*Melaleuca quinquenervia*), with more than 40 % of the total stem number, but also with wind- (*Alstonia costata, Geissois racemosa*) and bird-dispersed (*Guioa villosa*, *Cupaniopsis* spp.) early secondary successional forest species (pioneer species). These co-dominant species were associated to others early (*e.g. Fagraea berteroana*, *Pittosporum simsonii*) or late (*e.g. Garcinia* sp., *Dysoxylum* sp.) secondary successional forest species (Figure 5.2 and Table 5.2) (and see Ibanez *et al.* submitted-c). Conversely, the second site was widely dominated by *Codia albicans* (with more than 80 % of the total stem number) and *Melaleuca quinquenervia* was poorly represented (Figure 5.3 and Table 5.2).

5.3 Results and discussion

5.3.1 Co-dominated secondary successional forest

This first site represented an ongoing re-colonisation of forest on a savanna by pioneer forest species. As a result, the point-pattern of site 1 was heterogeneous with a gradient of density along the Y-axis (due to a density gradient pioneer species) while the density of *Melaleuca quinquenervia* was rougthly homogeneous (Figure 5.5). On the 238 *M. quinquenervia* inventoried in the whole area, more than 30 % were dead. The DBH structure of the alive *M.quinquenervia* population highlighted a low recruitment (Figure 5.6). Both observations suggested that the *M. quinquenervia* population is progressively disappearing.

We assumed that the mortality of *M. quinquenervia* was due to its shade intolerance, when shaded by other species (Ibanez *et al.* submitted-c; Serbesoff-King 2003). Hence, we hypothesised that the death was higher for the most shaded trees (*i.e.* the smallest trees or those being surrounded by tree dense structure). To test this hypothesis, we analysed the mortality variance of *M. quinquenervia* according to both their DBH (as proxy of the height) and local tree density (in a 5 m surrounding window) using a logistic regression approach. These variables weakly explained the variation

observed in the mortality of *M. quinquenervia* (*ca* 95 % of the variance remained unexplained Table 5.3). However, the proportion of dead trees was higher for small trees than large ones (Figure 5.7).

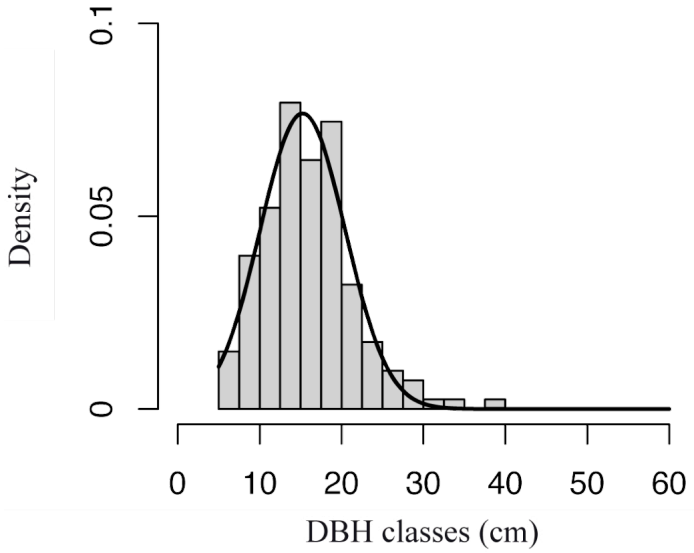

Figure 5.6 *Melaleuca quinquenervia's population DBH structure.*

Table 5.3 *Analysis of co-variance of M. quinquenervia mortality*

	Df	Sum. Sq.	% Var.	F value	P value
DBH	1	5.201	3.0	5.0979	*
Local density	1	0.0004667	0.0	0.0005	
DBH:Local density	1	5.026	2.9	4.9264	*
Residuals	158	161.18	94.1		

"*", $P < 0.05$; "**", $P < 0.01$; "***", $P < 0.001$

The estimated *L*-function for both all *M. quinquenervia* and alive ones only exhibited significant clustering in the range of 2-13 m and 5-13 m, respectively (Figure 5.8.A and B), while dead ones tended (but not significantly), to be clustered in the range of 2-5 m (Figure 5.8.C) suggesting density-dependent mortality. Alive and dead trees were randomly distributed relatively to each others (Figure 5.8.D).

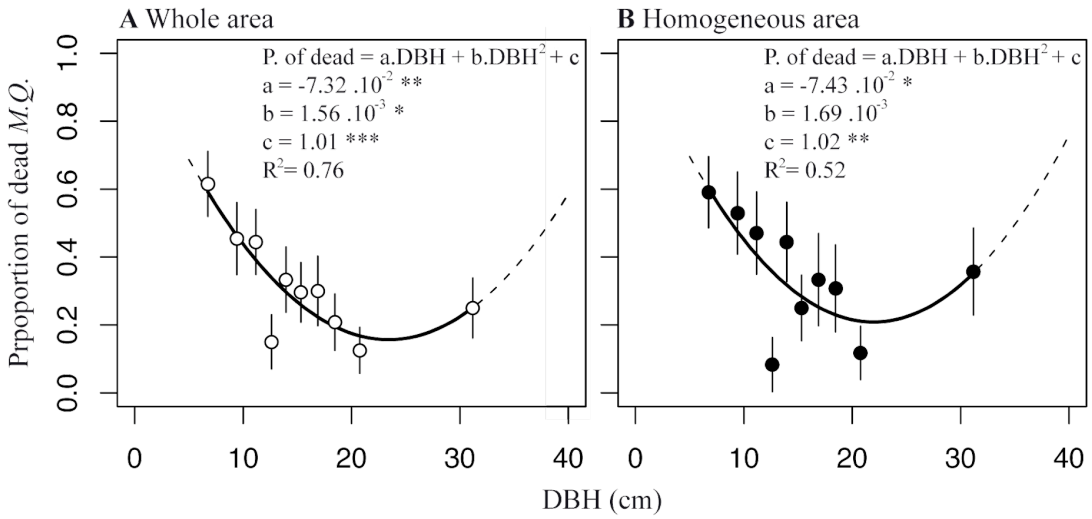

Figure 5.7 *Proportion of dead Melaleuca quinquenervia according to the DBH class. DBH classes correspond to deciles, bars represent 95 % CI and the black solid lines correspond to the polynomial fit for (A) the whole area and (B) the homogeneous area (see* Figure 5.5 *grey area).*

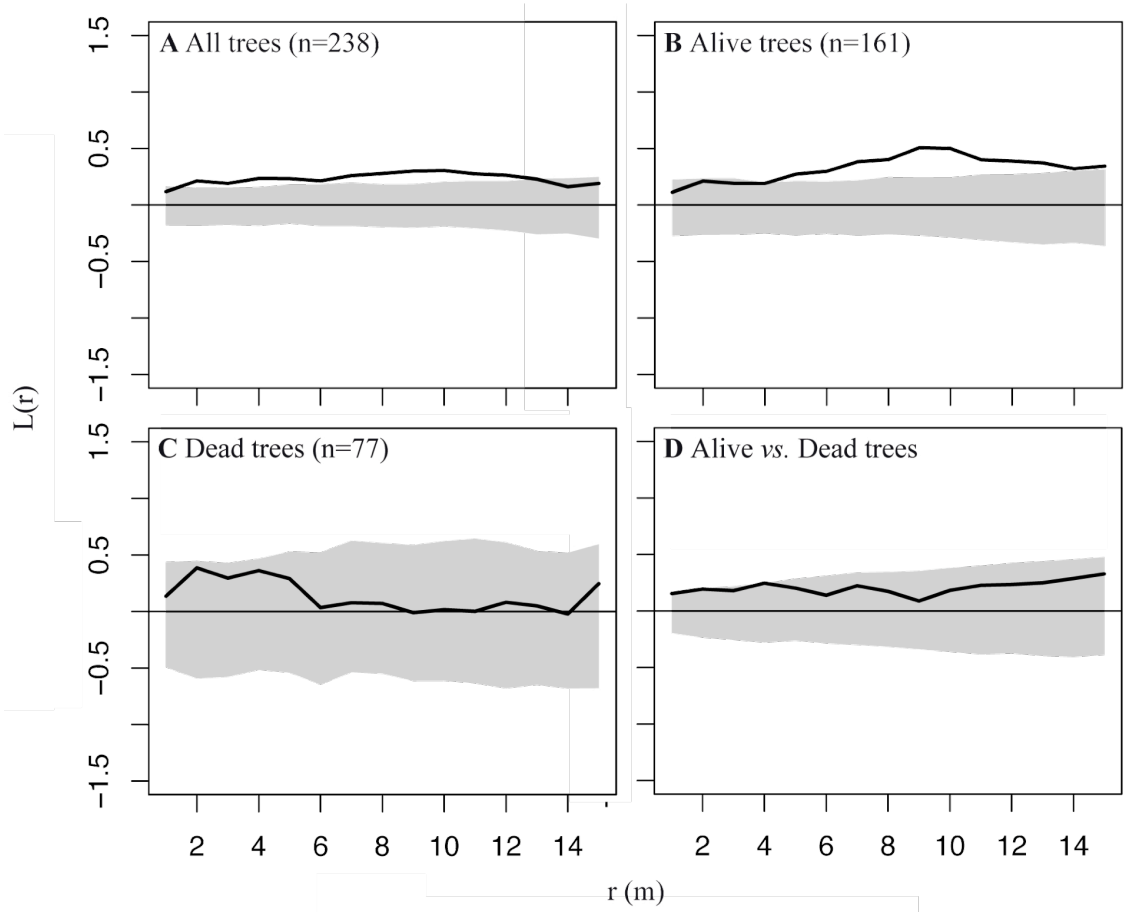

Figure 5.8 *Spatial point patterns of the Melaleuca quinquenervia population characterised by the L-function for the pattern of (A) all trees together, (B) only alive trees, (C) only dead trees and (D) alive and dead trees interaction (L_{12}-function).*

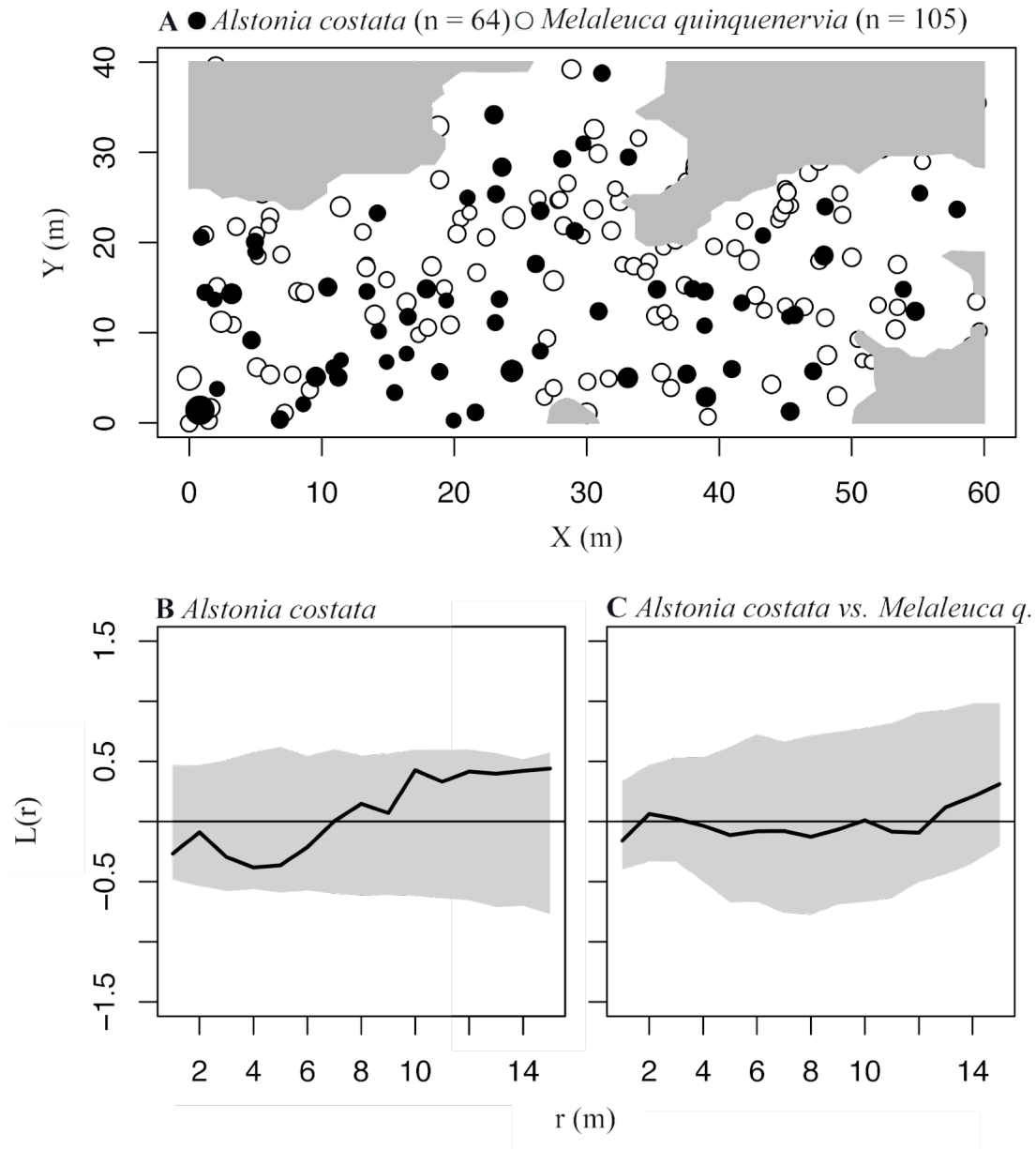

Figure 5.9 *Spatial point patterns of the Alstonia costata population. (A) Map of the Alstonia costata and Melaleuca quinquenervia trees (circles are proportional to the DBH), grey areas represent the areas removed to obtain stationary Alstonia costata point pattern. L-function for the patterns of (B) Alstonia costata and (C) Alstonia costata and Melaleuca quinquenervia trees interaction (L_{12}-function).*

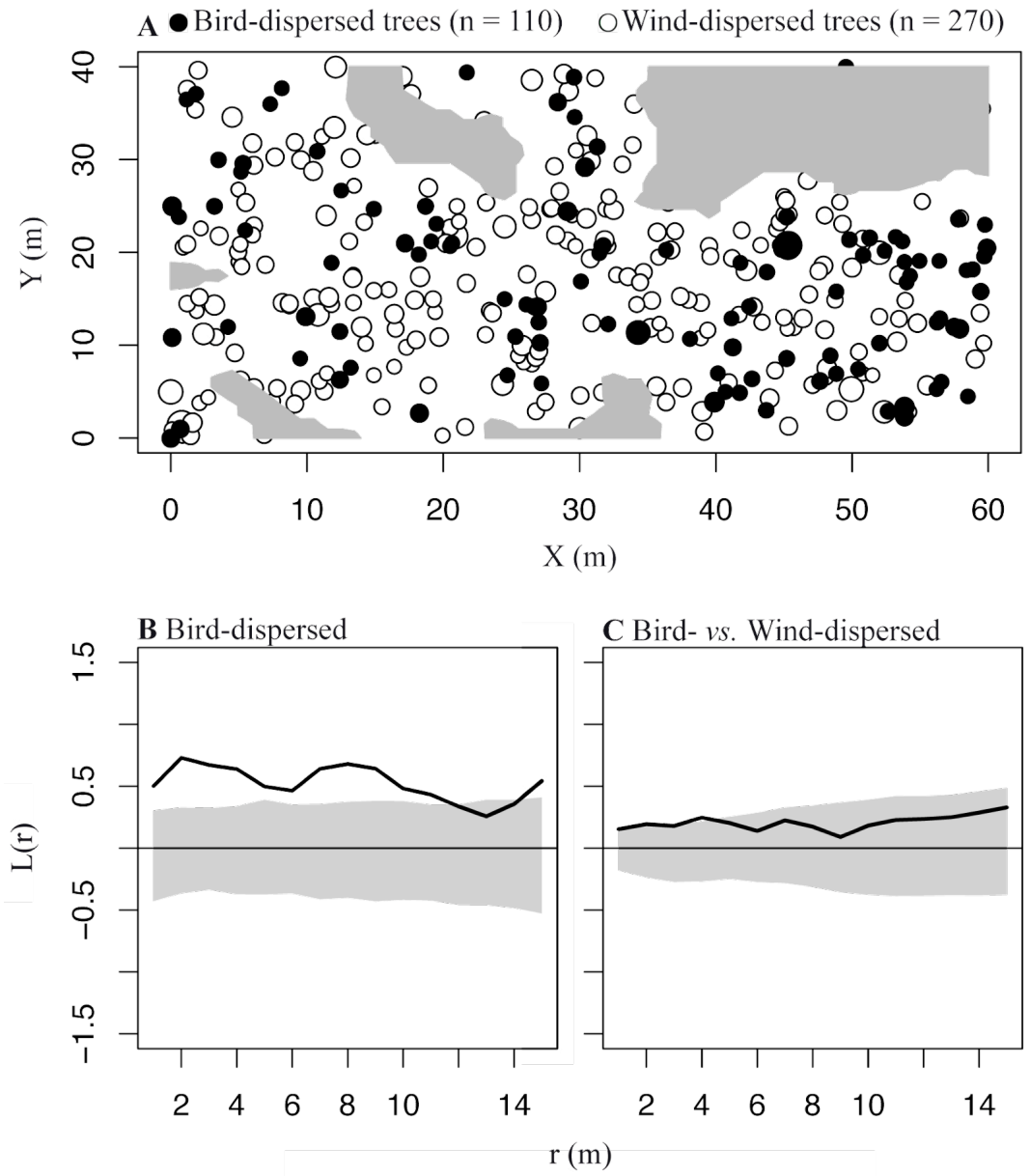

Figure 5.10 *Spatial point patterns of the bird-disepersed population. (A) Map of the bird-disepersed and wind-disepersed trees (see Table 2, circles are proportional to the DBH), grey areas represent the areas removed to obtain stationary bird-disepersed point pattern. L-function for the patterns of (B) bird-disepersed trees and (C) bird-disepersed and wind-disepersed trees interaction (L_{12}-function).*

To analyse the pattern of *Alstonia costata,* which was not homogeneous on the site, we used the method described by Pelissier & Goreaud (2001) to isolate the area where the density of *A. costata* could be assumed homogeneous (Figure 5.9.A). Although the pattern observed for *A. costata* did not significantly differ from CSR patterns (Figure 5.9.B), *A. costata* trees tended to repulse each others in the range of 0-7 m (regularity) and to attract each other's further. This classical pattern suggests repulsion close to the trees, due to competition (density-dependent mortality of juveniles), and attraction further on, due to dispersal limitation. During the savanna colonisation by *A. costata*, the establishment of the population of *A. costata* was likely independent from the position of the *M. quinquenervia* trees. Indeed, according to the estimated L_{12}-function *A. costata* and *M. quinquenervia* were randomly distributed relative to each others (Figure 5.9.C). We could not analyse the specific spatial pattern of the other species due to the lack of individuals per species. However, we analysed the spatial pattern of bird-dispersed species pooled together (see Figure 5.10.A), which were significantly aggregated in the range of 0-12 m (Figure 5.10.B) and tended to be aggregate with wind-dispersed ones in the range of 0-4 m (Figure 5.10.C). This pattern may be due to particular dispersal patterns such as perch effect (Ibanez *et al.* in prep.-a) or facilitation processes (e.g. Halpern *et al.* 2010).

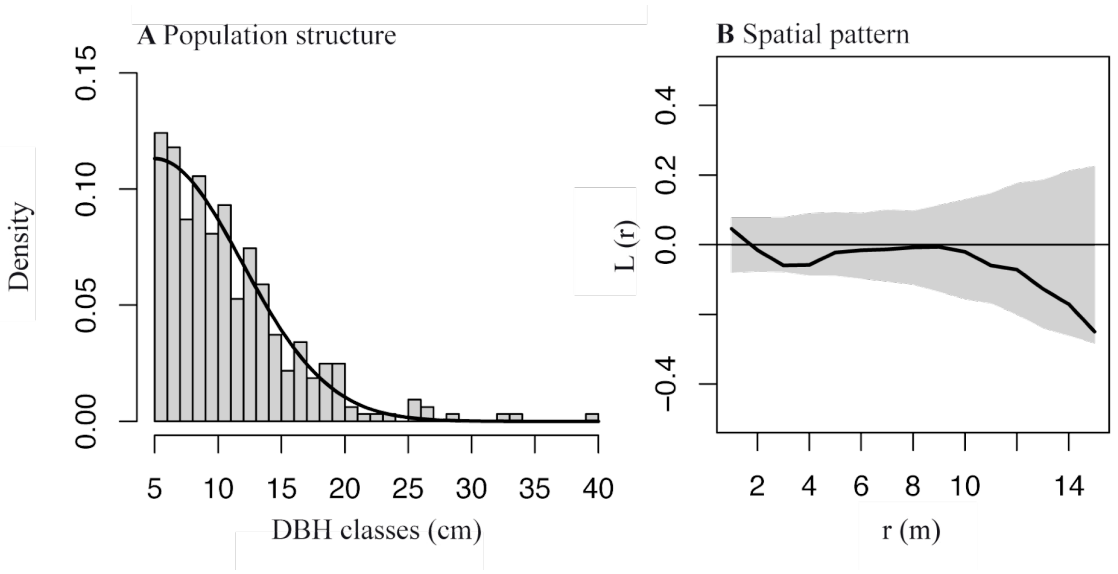

Figure 5.11 *Codia albicans's population structure. (A) DBH population structure and (B) spatial pattern described by the estimated L-function.*

5.3.2 Monodominated secondary successional forest

The second site represented a relatively homogeneous secondary successional forest dominated by *Codia albicans* where the population of *M. quinquenervia* had almost disappeared (Ibanez *et al.* submitted-c). The population of *C. albicans* was growing up with high tree recruitment (Figure 5.11.A). The global spatial pattern of the *C. albicans* population spatial pattern did not differ from CSR (Figure 5.11.B). However, we hypothesised that the successive establishment of tree cohorts may result in a spatial structure that differs from CSR possibly due to intra-specific competition. To test this hypothesis, we split the *C. albicans* population into two cohorts, called "young" and "adult", according to different DBH thresholds and we tested the independence of the two-associated point patterns. The estimated L_{12}-function showed that from a threshold of *ca* 12 cm in DBH, the young and adult trees were not independently distributed (Figure 5.12.A). Considering the 90 % quantile as threshold (17.7 cm), there was a significant repulsion between young and adult trees in the range of 0-6 m (Figure 5.12.B) and young trees tended to be aggregated (not shown). However no significant spatial dependence between *C. albicans* and the others species or groups of species was observed (not shown).

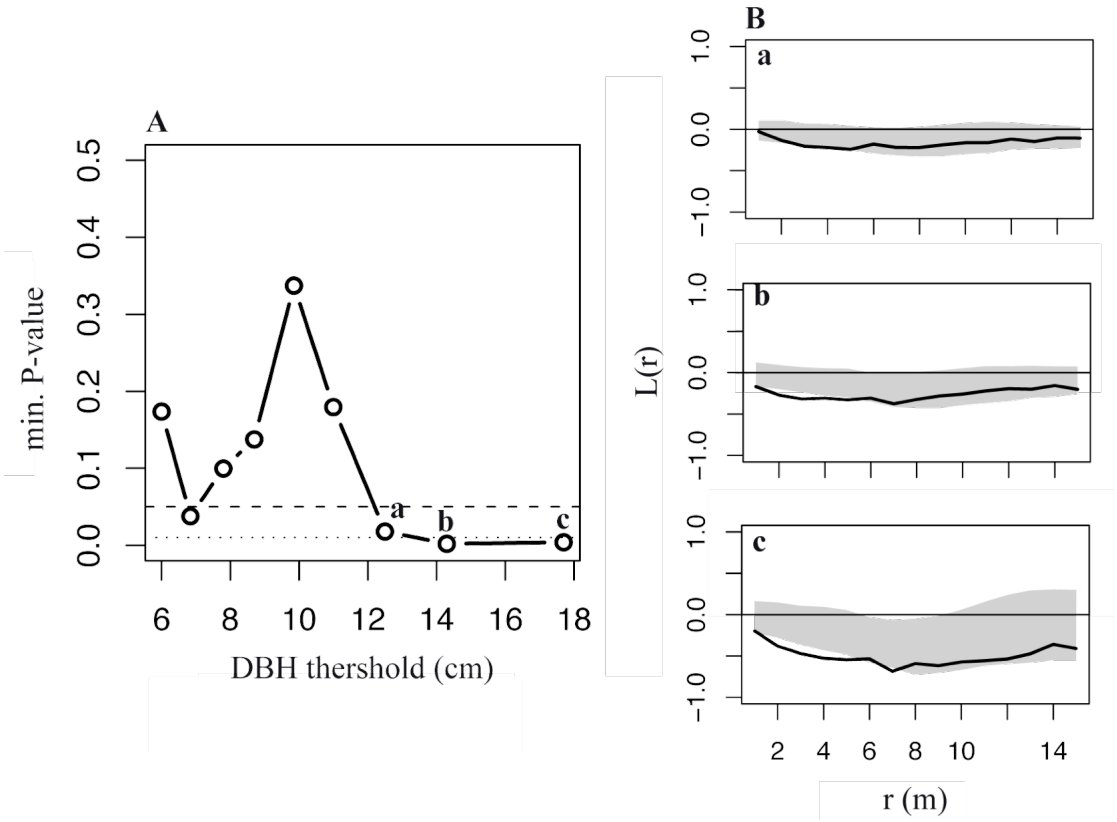

Figure 5.12 *Spatial point patterns of the Codia albicans population. (A) minimal local P-value of departure from a Poisson pattern (CSR) for L_{12}-function that characterise the interaction between "young" and "adult" trees, which were discriminate according to a DBH threshold (horizontal dashed and pointed lines represent the significant threshold for alpha = 0.05 and alpha = 0.01, respectively). (B) L_{12}-function for the interaction between "young" and "adult" for different threshold (a, b and c).*

5.3.3 Conclusion

Point pattern analysis is a good framework to study plants interactions, however such analysis required large homogeneous areas and numerous individuals per species to obtain exploitable and robust results. Such dataset are difficult to obtain in our case due to the inhomogeneity of most of secondary succession zones and to the low number of individuals per species. Nevertheless, these preliminary results point out differences between the pattern of secondary succession dominated by *Codia albicans* and the others. The early colonisation by *Codia albicans* likely conduces to a fast closure of the

savanna, which may prevent the establishment of other pioneer species. Conversely, in other secondary successional patterns, the closure of the savanna is likely more gradual leading to a slower replacement of savanna dominant trees (*Melaleuca quinquenervia*) and allowing the establishment of a more diverse floristic assemblage. More studies are needed to understand the inter-specific competition / facilitation processes leading to these to different secondary successional patterns.

6 Estimated fire injuries highlight low fire tolerance of New Caledonian savannas trees

This section is submitted (since August 25th 2011) to *Journal of Vegetation Science* as the following research paper :

Ibanez, T., Curt, T., Gaucherel, C., and Hély, C., (submitted). Estimated fire injuries highlight low fire tolerance of New Caledonian savannas trees, submitted to *Journal of Vegetation Science*.

6.1 Résumé

Questions : Quelles sont les différences de tolérances aux feux de surfaces des espèces de début de succession secondaire ? Quels sont les implications en terme de dynamiques forêt–savane et de gestion du paysage ?

Localisation : Les savanes anthropiques situées dans le point chaud de biodiversité Néo Calédonien (Pacifique sud-ouest).

Méthodes : La variabilité de l'intensité des feux de savane en Nouvelle Calédonie a été estimée à partir de mesure de combustible de terrain et d'un modèle de comportement du feu. A partir de ces intensités, les dégâts théoriques au cambium et à la couronne des arbres ont été estimés pour 11 espèces comprenant l'espèce dominante des savanes Néo-Calédoniennes (*Melaleuca quinquenervia*) et des espèces de début de succession secondaire. Pour chacune de ces espèces, les dégâts au cambium ont été estimés à partir de la profondeur de nécrose (fonction de l'intensité et du temps de résidence des feux) et l'épaisseur de l'écorce, et les dégâts à la couronne ont été estimés à partir de la hauteur de roussissement (fonction de l'intensité des feux) et de la hauteur des arbres. Ensuite, les modèles de croissance d'épaisseur d'écorce et de hauteurs des arbres ont été confrontés aux potentiels de tolérances aux feux des différentes espèces étudiées.

Résultats : Les 11 espèces étudiées ont présenté de fortes différences dans leurs capacités à éviter les dégâts causés par les feux au cambium. Ces différences sont liées à différents modèles de croissance et d'investissement dans la production d'écorce. Cependant, toutes les espèces étudiées sont très exposées aux dégâts causés à la couronne à cause d'un faible investissement dans la croissance en hauteur. Globalement, la partie aérienne de la plupart des individus mesurés serait tuée par des feux de faible intensité (1000 $kW.m^{-1}$) qui semble être fréquent dans les savanes Néo-Calédonienne selon nos mesures et simulations.

Conclusion : Les espèces se début de succession secondaire poussant dans les savanes Néo-Calédonienne semblent peut adaptées aux feux comparées comparé à ce qui est observé dans les savanes à l'échelle du globe. Ainsi, les jeunes plants de ces espèces peuvent difficilement atteindre leurs tailles adultes dans les zones soumises aux incendies. Cependant, l'utilisation des espèces les plus tolérantes aux feux et une

meilleur gestion des incendies peuvent être deux voies complémentaires pour gérer les paysage afin de conserver la biodiversité et les services éco-systémiques liés aux forêts.

Mots clés: Relations allométriques; épaisseur d'écorce; dommages au cambium; dommages à la couronne; taille d'échappement; comportement du feu; feux de surface; mortalité; hauteur des arbres.

6.2 Abstract

Questions: How early secondary successional species differ in their tolerance to surface fires? What impacts of these fire tolerances for savanna-forest dynamics and landscape management?

Location: Anthropogenic savannas located in the New Caledonian biodiversity hotspot (south western Pacific).

Methods: We estimated the range of fire intensity in New Caledonia savannas using field survey of fuels and a fire behaviour model. In this range of fireline intensity, we assessed theoretical fire injuries on cambium and crown for 11 species encompassing the dominant tree of New Caledonia (*Melaleuca quinquenervia*) and early secondary successional species. Using empirical models, we estimated for each species the cambium damage from depth of necrosis (as a function of fireline intensity and fire residence time) and bark thickness, and the crown damage from scorch height (as a function of fireline intensity) and tree height. We compared bark thickness and tree height increment patterns among species and the potential fire tolerance.

Results: The 11 species had very contrasting capacity to avoid fire injuries on bole cambium due to differences in bark investment patterns whereas they were all very exposed to scorching and crown injury. Globally most of the sampled individuals were likely top-killed by low intensity fire (1000 $kW.m^{-1}$), which are frequent according to our simulations.

Conclusions: The early secondary successional species growing in New Caledonian savannas were poorly adapted to fire in comparison with the literature on worldwide savanna's trees. As a result theirs juveniles could difficultly reach the adult size in a fire prone area. Restoration using the most fire-tolerant species and fire management may be complementary ways to manage the landscape in order conserve biodiversity and ecosystems services.

Keywords: Allometric relationships; bark thickness; cambium damage; crown damage; escape size; fire behaviour; surface fires; top-kill; tree height.

6.3 Introduction

Savannas are characterised by a continuous grass layer with a discontinuous tree cover (Scholes and Archer 1997) making them very flammable and supporting high fire frequency (Hély and Alleaume 2006). Surface grass fire is one of the main disturbances with grazing that interact with rainfalls to limit trees in savannas, allowing tree and grass to coexist (Bond 2008; Bond and Keeley 2005; Staver *et al.* 2011a). In New Caledonia (Ibanez *et al.* submitted-b; Jaffré *et al.* 1998), as in others places in the tropics (e.g. Cavelier *et al.* 1998; Veldman and Putz 2011), forest exposed to anthropogenic and environmental changes may shift to savanna causing large losses of biological, ecological and economic resources (Folke *et al.* 2004; Scheffer and Carpenter 2003). Assessing the fire tolerance of woody species growing into savannas is critical to understand the forest-savanna dynamics to manage and conserve biodiversity and associated ecological services.

During surface fires, fuel (mainly grasses in savannas) combustion transfers heat to the trees and injure roots, boles, stems and crowns (see physical processes described by Michaletz and Johnson 2007). The degree of these injuries is determined by both fire behaviour and tree characteristics (Whelan 1995). Fireline intensity and fire residence time – describing the rate of heat or energy released by the fire front and the time of heating, respectively – are important fire behaviour characteristics widely used to predict stem mortality (e.g. Michaletz and Johnson 2008; Ryan and Reinhardt 1988; Williams *et al.* 1999). Bark thickness and the height of the tree crown are considered as the most important tree traits as both isolate critical tissues from heating and are used as predictor of tree mortality (e.g. Bond 2008; Higgins *et al.* 2000; Hoffmann and Solbrig 2003; Pinard and Huffman 1997). Indeed, a thick bark isolates the vascular cambium (lateral meristem) that produces the vascular tissues (see Bauer *et al.* ; Dickinson and Johnson 2004; Gashaw *et al.* 2002; van Mantgem and Schwartz 2003). Likewise, a high crown base likely isolates vegetative buds (apical meristems) that produce branches, bud foliage and reproductive organs (see Michaletz and Johnson 2006; Van Wagner 1973), while belowground meristems are isolated by soil layer.

Bark thickness and tree crown base height constitute defences against fire that are largely dependent on stem diameter, allowing large (mature) individuals to be less

injured by fire than small (juveniles) ones (e.g. Hoffmann *et al.* 2009; Hoffmann *et al.* 2003). Thus, during a savanna fire most of the small individuals are top-killed (*i.e.* their aboveground biomass is killed) while their root system often survives and allows most of them to persist by basal resprouting (Bond and Midgley 2001). Juveniles have to reach the so-called "escape size" allowing them to avoid fire top-kill to recruit in the mature size, however in savannas that can burn every year, they may be caught in a "fire trap" if the interval between two fires is too short to reach this size (Higgins *et al.* 2000; Scutz and Bond 2009).

Confronted to such fire disturbance regime, trees can either invest in growth to reach their "escape size" to resist to fire, or invest in belowground reserves to allow them to resprout after top-kill to persist. Actually, an evolutionary trade-off exists between these two investments according to the regeneration strategy – obligate seeders, facultative seeders, and obligate resprouters – and environmental conditions (Gignoux *et al.* 1997; Scutz and Bond 2009; Vesk 2006). Although resprouting may allow species to persist in a fire-prone ecosystem, the time required to reach the escape size, allowing or not a species to reach its mature size in fire prone ecosystems, is a critical trait (Gignoux et al. 2009).

Allometric relationships between the stem diameters and the sizes of the fire defences (namely bark thickness and tree crown base height) offer a good framework to characterise and analyse the different patterns in defence investment along plant life (Jackson et al. 1999). Escape sizes are widely determined by post-fire confrontation of defence size, top-kill or mortality *via* survival analysis (e.g. Bond 2008; Hoffmann and Solbrig 2003; Lawes *et al.* 2011). Such data on post fire tree mortality are difficult to measure for a wide range of tree species and stem diameter (size class) in New Caledonian savannas supporting high fire frequency that limit tree establishment and growth. Moreover, as mentioned above, top-kill or mortality probability is a function of tree characteristics and fire behaviour, the latest being unknown for most post-fire studies.

In this study, we assessed the escape size of 11 woody species encompassing the dominant savannas species (*Melaleuca quinquenervia*) and early secondary species (Ibanez *et al.* submitted-c) using allometric relationships and theoretical fire injuries. We used field surveys of savanna fuels (Hély, unpublished data) to simulate the likely

range of fireline intensity and fire behaviour in New Caledonian savannas using the BehavePlus semi-empirical model. We hypothesized that the fire tolerance of the studied species is highly variable according to species-specific traits allowing resisting or avoiding fire effects, in particular difference in investment in bark and height. Almost all species should reach the size to survive to low-intensity surface fires but small trees species or species that develop fire resistance along their life cycle are hypothesized to resist less or poorly to the most intense surface fires.

6.4 Materials and methods

6.4.1 Study site

New Caledonia (NC), located in the south Pacific just above the Tropic of Capricorn, 1500 km eastward of Australia and 2000 km northward New Zealand (between 20°-23°S and 164°-167°E, Figure 6.1), is one of the smallest (*ca* 19 000 km^2) worldwide biodiversity hotspot (Mittermeier *et al.* 2004; Myers 1988). Its flora is particularly rich according to little size of the archipelago, with 3371 native vascular species and high level of endemism reaching 75 % (Morat et al. Submitted) supported by a particular geological history (Grandcolas *et al.* 2008) and a mosaic of ecosystems linked to different edaphic substrates, rainfalls and human activities (Jaffré *et al.* 1998; Pillon *et al.* 2009). However, more than half of the original vegetation is already destroyed (Jaffré et al. 1998). The rainforest, replaced by anthropogenic formation such as savannas, is rare and fragmented at low and middle elevation, therefore restricted to high elevation or inaccessible areas (Jaffré *et al.* 1998; Jaffré and Veillon 1994). Bush fires, maintaining the savannas and eroding rainforest edge, are one of the main threats for the New Caledonian biodiversity (Pascal et al. 2008).

New Caledonian savannas, dominated by *Melaleuca quinquenervia* (Myrtaceae) locally known as "*niaouli*", cover *ca* 30 % of the main island in majority along the West coast side, which is drier than the East one (see Figure 6.1). The sampling was performed into savannas located on the west side of the *Aoupinié* mountain in the

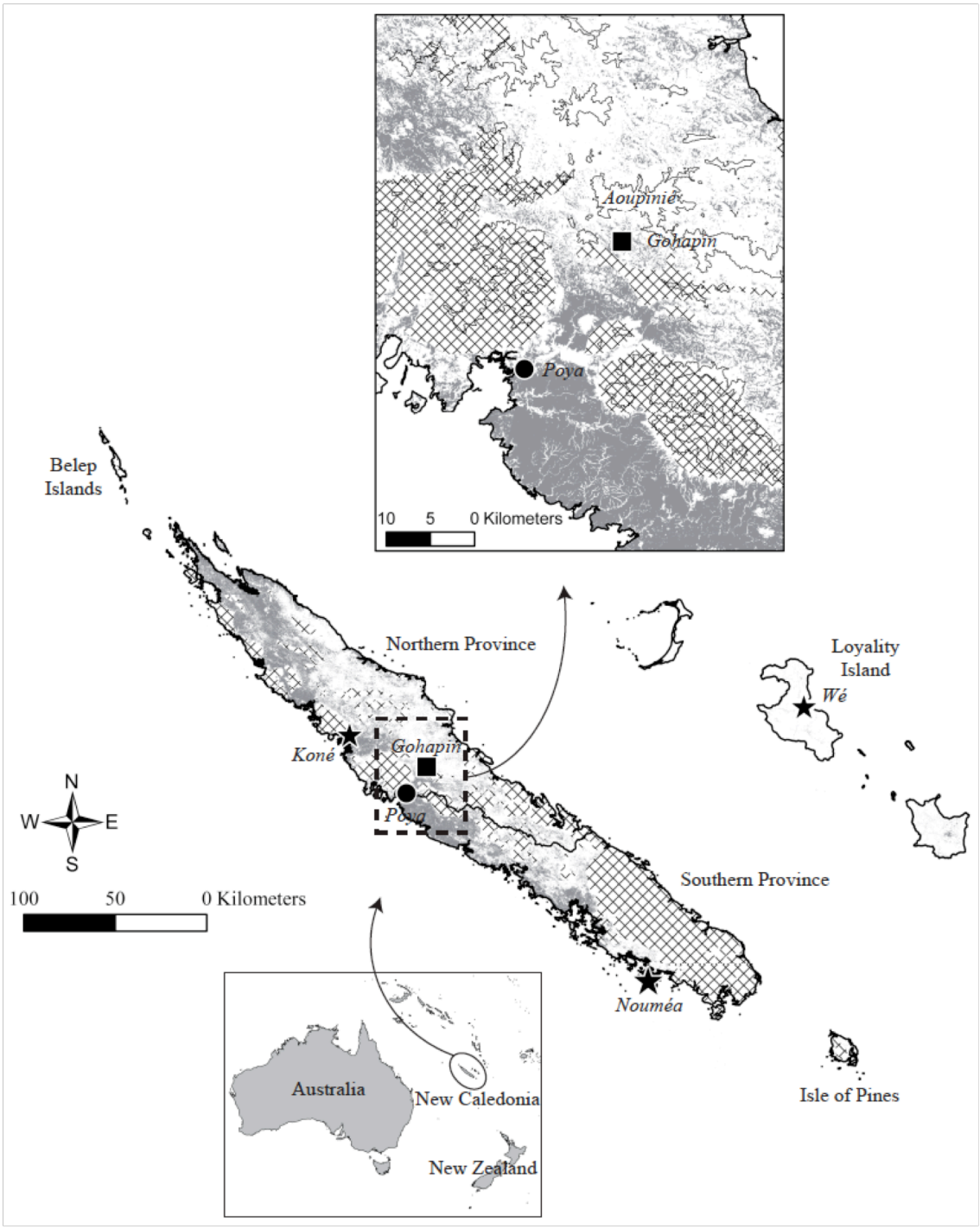

Figure 6.1 Location of the studied area. Sampling were performed on the western side of the Aoupinié (1006 m) between the Gohapin tribe and Poya in the middle of the New Caledonian main island. Grey areas represent the savannas areas (from SGT 2008) and hatched areas represent the ultramafic substrate encompassing peridotite and serpentinite (from Fritsch 2011). In the insite, contours represent the areas > 500 and 1000 m asl.

surroundings of the *Gohapin* tribe in areas receiving between 1500 and 3000 mm rainfall per year (METEO-France 2007). The landscape is a mosaic of remnant forests and savannas (see Ibanez et al. submitted). The climate of NC is tropical oceanic with a cool and a hot season, both overlapping with a characteristic dry season from August to November. This season, characterised by low rainfall, increasing temperature and *alizé* east trade winds blowing almost permanently, corresponds to the bush fire season.

6.4.2 Species selection

We compared fire tolerance traits of 11 species (6 endemics and 5 autochthonous, see Table 6.1) naturally occurring in New Caledonian savannas selected by field survey and community analysis (see Ibanez *et al.*, submitted). They comprise the dominant tree species of New Caledonian savannas, *Melaleuca quinquenervia* and early secondary-forest species encompassing both trees and small tree. Seven out of eight represented families are widespread in tropical and sub-tropical regions (*Apocynacece*, *Loganiaceae*, *Moraceae*, *Myrtaceae*, *Pittosporaceae, Rutaceae,* and *Sapindaceae*) and one is predominantly restricted to southern hemisphere (*Cunoniaceae*).

6.4.3 Fire resistance traits & allometric relationships

We selected and measured three morphological traits that affect fire tolerance; the bark thickness (BT) that affects cambium injuries, the tree height (TH) and the tree crown base height (CBH) that both affect tree crown injuries and the associated diameter at breast height (DBH). In a nutshell, the thicker is the bark and the higher is the crown base, the least are fire injuries (see Michaletz and Johnson 2007).

We measured these morphological traits on individuals located into savannas or open early secondary successional forest that did not shown recent fire marks. BT was estimated by the mean of two bark gauge measures (1 mm accuracy) at two random opposite points at breast height. In the literature, BT is measured either at 0.3 m (e.g. Hoffmann *et al.* 2003; Hoffmann and Solbrig 2003) or at 1.3 m (e.g. Gashaw *et al.* 2002; Van Nieuwstadt and Sheil 2005), however Barlow and Peres (2008) showed that

Table 6.1 *Studied species*

Family	Species	Code	Status[†]	Biological type
Apocynaceae	*Alstonia costata* (G. Forster) R. Brown	AC	E	Tree
Apocynaceae	*Tabernaemontana cerifera* Pancher & Sebert	TC	E	Small tree
Cunoniaceae	*Codia albicans* Vieill.	CA	EE	Tree
Cunoniaceae	*Geissois racemosa* Labill.	GR	EE	Tree
Loganiaceae	*Fagraea berteroana* A. Gray	FB	A	Small tree / Epiphyte
Moraceae	*Ficus habrophylla* Bennett ex Seemann	FH	A	Small tree
Myrtaceae	*Melaleuca quinquenervia* (Cav.) S.T. Blake	MQ	A	Tree
Pittosporaceae	*Pittosporum simsonii* Montrouz.	PS	E	Tree
Rutaceae	*Acronychia laevis* Forster &G. Forster	AL	A	Small tree / Shrub
Sapindaceae	*Elattostachys apetala* (Labill.) Radlk.	EA	A	Tree
Sapindaceae	*Guioa villosa* Radlk.	GV	E	Small tree

[†] EE for endemic genus, E for endemic species and A for autochthonous species

BT was non-significantly different at 0.3 and 1.3 m for non-buttressed trees such as those we studied. For individuals with fissured bark, measurements were made at the ridges. TH and CBH (lower branch of the crown) were measured using an ultrasonic hypsometer (Vertex 4) with 0.1 m accuracy.

We computed the allometric relationships between the DBH and BT, TH or CBH to compare the species' investment in these morphological traits along their growth using the following equation:

$$BT, TH, CBH = \beta \times DBH^{\alpha} + \varepsilon$$

where β is a proportionality coefficient, α is the allometric coefficient and ε is the error. The allometric coefficient α can be interpreted as an allocation coefficient, that is, if $\alpha >$ 1 (positive allometry) the investment in bark or height growth is disproportionally greater at large DBH, if $\alpha < 1$ (negative allometry) the investment in bark or height growth is disproportionally greater at small DBH and if $\alpha \approx 1$ the investment in bark or height growth is proportional to the increment in DBH (Jackson et al. 1999). We used least-squares regression to fit allometric relationships on log-transformed data and estimate α.

6.4.4 Fire behaviour in New Caledonian savannas

Fire-induced injury is a function of both tree characteristics (morphological traits measured and described above) and fire behaviour. However, fire behaviour in the different New Caledonian ecosystems is poorly known (to our knowledge, none field observations on fire behaviours exist in NC). Given that, we chose to characterise New Caledonians savannas' fire behaviour using BehavePlus 4.0.1 fire behaviour model (Andrews et al. 2008).

BehavePlus calculates fire behaviour variables such as fire line intensity (I), rate of spread (ROS) and flame length (FL) from fuels, weather and topography. Fuels were implemented with data from 29 New Caledonian savanna stands (see Appendix) from different localities in the New Caledonian main island. Then, fire behaviour characteristics (I, ROS and FL) were calculated for the 29 available fuel-types with

winds from 0 to 30 km.h^{-1} for slopes of 5 % and 30 % (*ca* 90 % of the New Caledonian savanna are present on 30 % slopes or less) and for a dry and medium fuel moisture scenarios (Table 6.2).

Table 6.2 *Fuel moisture scenarios used for BehavePlus simulations.*

Moisture scenarios	Dead fuel moisture content (%)			Live fuel moisture content (%)		
	1H	10H	100H	Herbaceous	Woody	Canopy leaves
Dry	5	10	15	70	90	100
Medium	10	15	25	90	120	100

According to BehavePlus simulations, savannas trees were likely to be exposed to a wide range of fireline intensity (I, see Figure 6.2.). Simulated I range from < 10 to ≈ 2000 kW.m^{-1} (95 % CI) under lowest wind speed condition to ≈ 75.0 to ≈ 13500 kW.m^{-1} (95 % CI) under highest wind speed condition with rate of spread ranging from 0.1 to 3.4 m.min^{-1} (95 % CI) and 0.8 to 27.4 m.min^{-1} (95 % CI) and flame length ranging from 0.2 to 2.5 m (95 % CI) to 0.5 to 6.1 m (95 % CI), respectively. Few field data on savanna fires intensity are available in the literature to validate our simulations, however simulated I were of the same order than those published (from 25 to 22000 kW.m^{-1}, see Table 6.3) with comparable fuel loads (from 0.11 to 25.10 t.ha^{-1} in this study vs. 0.83 to 14.20 t.ha^{-1} in the literature).

6.4.5 Estimated fire injuries

Potential fire injuries on (i) bole cambium (depth of necrosis) and (ii) tree crown (scorch height) were estimated from fireline intensity (I) using empiric models.

(i) Experimental studies shown that although inter-specific variation in bark moisture, density, structure or composition may affect the insulating capacity of bark, bark thickness is the main parameter determining fire resistance (Bauer *et al.* 2010; Dickinson and Johnson 2004; Gashaw *et al.* 2002). Thus, the depth of necrosis (*i.e.* the

depth where T > 60°C) is widely estimated from data on the heating source (e.g. Michaletz and Johnson 2008; Peterson and Ryan 1986). We estimated the depth of necrosis (D_n in mm) using the model developed by Bova and Dickinson (2005) as it combines both I (in $kW.m^{-1}$) and residence time (R_t in s) as follows:

$$D_n = 0.21 \times I^{0.20} \times R_t^{0.64}$$

We estimated estimate D_n and explored the tolerance of trees to fires with assumed R_t of 60 s (Figure 6.3.a). This R_t seemed reasonable according to the few available data on R_t in savanna fires (Savadogo *et al.* 2007; Stocks *et al.* 1996).

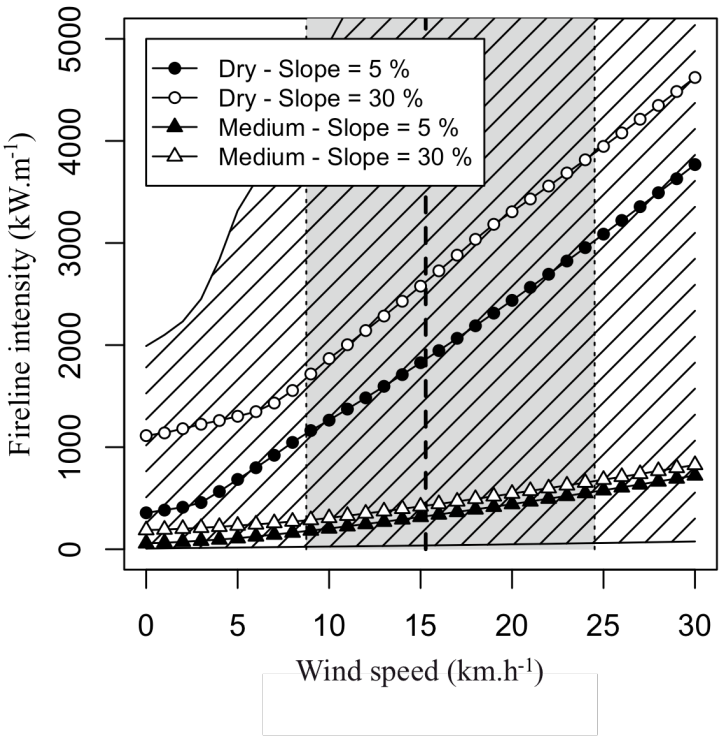

Figure 6.2 *Simulated savanna fires fireline intensity (I) for several realistic scenarios of fuel moisture (dry and medium), slope (5 % and 30 %) and wind speed (from 0 to 30 km/h). Symbols represent the median of I for different scenarios. The hatched area represents a 95 % CI for all scenarios taken together. The vertical bold dotted line represents the median wind speed during dry season and the two vertical dotted lines represent the 0.25 and 0.75 quantiles.*

Table 6.3 *Comparison between this study and literature regarding fuel load and fireline intensity (I) ranges in savannas.*

References	Place	Nb. of fire	Fuel load ($T.ha^{-1}$)	I ($kW.m^{-1}$)
Gambiza *et al*. (2005)	Zimbabwe	15	-	25 – 1 341
Govender *et al*. (2006)	South Africa, Kruger National Park	956	0.83 - 9.21	28 – 17 705
Hely *et al*. (2003)	Western Zambia	8	3.56 - 5.95	43 – 9 476
Hoffa *et al*. (1999)†	Zambia, Western province	13	1.88 - 13.23	25 – 5 274
Kauffman *et al*. (1994)†	Brazil, Cerrado	2	7.13 - 10.03	2 842 – 16 394
Savadogo *et al*. (2007)	West Africa (Burkina Faso)	32	-	*ca* 250 – 2 750
Shea *et al*. (1996)	South Africa, Kruger National Park	10	2.22 - 5.49	480 – 6 130
Shea *et al*. (1996)	Zambia, Kasanga National Park	4	3.16 - 7.34	1 734 – 4 061
Smith *et al*. (2005)†	Botswana, Chobe National Park	9	2.00 - 9.93	130 – 9 474
Stocks *et al*. (1996)	South Africa, Kruger National Park	2	1.28 - 5.96	4 048 – 10 906
Vanwilgen and Wills (1988)†	South Africa, Hluhluwe / Umfolozi Park	10	1.60 - 14.20	194 – 5 993
Williams *et al*. (1998)	Australia, Northern territory	29	-	*ca* 1 000 – 22 000
Williams *et al*. (2003)†	Australia, Northern territory	25	2.10 - 9.80	500 – 18 000
All		1115	0.83 - 14.20	25 – 22 000
This study	New Caledonia		0.11 - 25.10‡	1 – 28 558

† in Govender *et al*. (2006)

‡ see Appendix

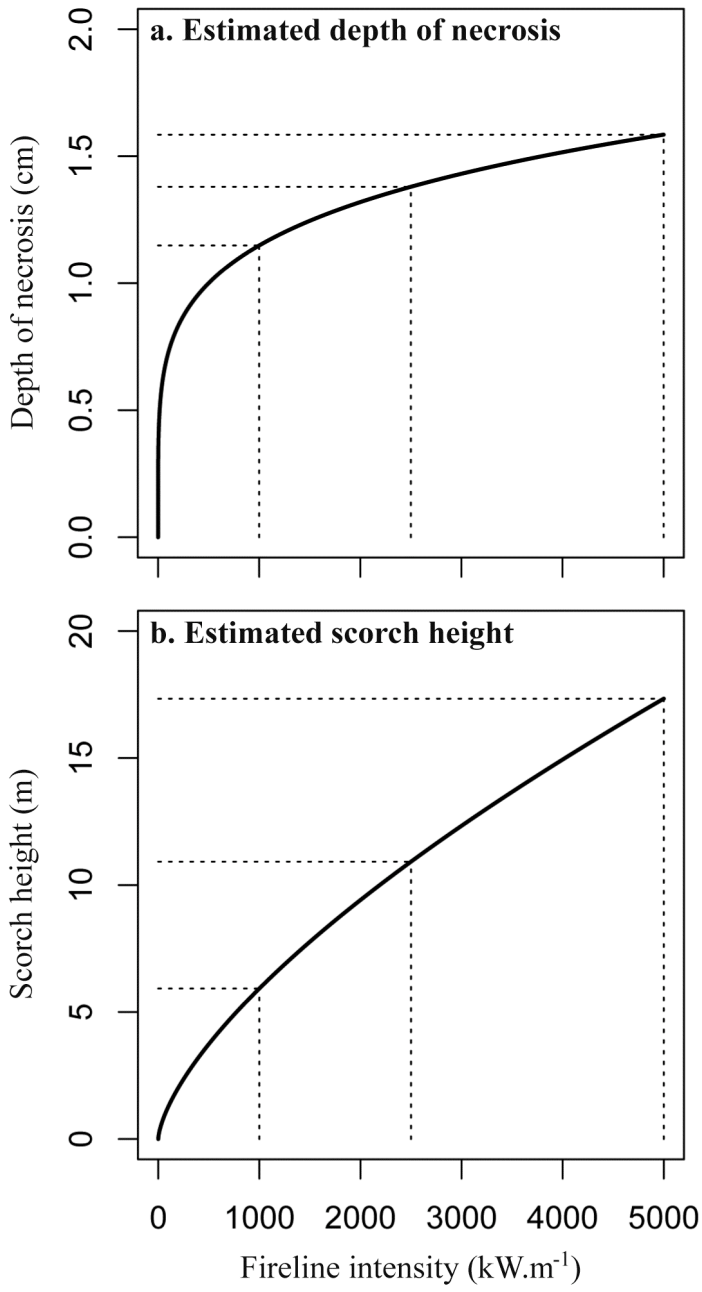

Figure 6.3 *Depth of necrosis (a) and scorch height (b) estimated from fireline intensity (I). The dotted lines show the values of depth of necrosis (1.15, 1.38 and 1.59 cm) and scorch height (5.9, 10.9 and 17.3 m) for I = 1000, 2500 and 5000 kW.m^{-1}, respectively.*

(ii) Height of scorch (H_{sc} in m) was estimated using the non-linear relationship between H_{sc} and I (Van Wagner 1973):

$$H_{sc} = k \times I^{2/3}$$

where k is an empirical coefficient measured from I and H_{sc} data. As we didn't have any data on scorch height in New Caledonia, H_{sc} was estimated with k = 0.154 (see Figure 6.3.b). This k parameter was approximated from the empiric relationship between H_{sc} and I ($H_{sc} = 21.2 - 17.6 \times e^{(-0.000287 \times I)}$) observed during fires in savannas of Northern Australia which are also a eucalypt savannas (Kapalaga experiment, see Williams et al. 1998).

6.5 Results

6.5.1 Species and DBH explained fire resistance traits variability

The studied morphological traits involved in fire tolerance were significantly determined by the species (Table 6.4), and bark thickness (BT) was the more specific trait. Indeed, the species and the stem diameters at breast height (DBH) explained together *ca* 75 % of the variance observed in BT and tree height (TH) while they explained less than 50 % of the variance in tree crown base height (CBH) which is likely more influenced by environmental factors (*e.g.* fires, browsing, competition with other trees or grasses). However, note that the species, affecting the architecture and the development of the canopy, explained *ca* 30 % of the variance in tree CBH. The species also explained more of the observed variance in BT than DBH did (48.3 and 24.1 %, respectively), while the opposite was found for the variance of TH (20.1 and 53.9 %, respectively).

Table 6.4 *Analyse of covariance between the studied morphological traits, the species and DBH.*

	Df	Sum. Sq.	% Var.	F value	P value
Bark thickness					
Species	10	15.2826	48.3	78.0235	***
ln(DBH)	1	7.6218	24.1	389.1228	***
Interaction	10	0.8343	2.6	4.2593	***
Residuals	405	7.9328	25.0	-	-
Tree height					
Species	10	6.4702	20.1	67.8978	***
ln(DBH)	1	17.3099	53.9	1816.4864	***
Interaction	10	0.2664	0.8	2.7951	**
Residuals	848	8.0809	25.2	-	-
Tree crown base height					
Species	10	6.0716	29.8	27.5298	***
ln(DBH)	1	3.0515	15.0	138.3615	***
Interaction	10	0.5159	2.5	2.3391	*
Residuals	488	10.7627	52.7	-	-

"*", $P < 0.05$; "**", $P < 0.01$; "***", $P < 0.001$

Table 6.5 *Estimated allometric coefficient (α) for the DBH-bark thickness relationship. Different letters show significant difference in α among species). Bark thickness at breast height is given in absolute (BT) and normalised (i.e. in percent of the stem radius NBT).*

Species	N	DBH	BT	Bark α				NBT (%)	
		range (cm)	range (cm)	Estimate	SE	P	R^2	Mean	SE
Acronychia laevis	13	5.0 - 7.2	0.20 - 0.85	1.59 a	0.39	**	0.62	15.6	3.7
Alstonia costata	67	5.2 - 55.4	0.10 - 1.00	0.54 b	0.06	***	0.50	8.1	2.5
Codia albicans	105	5.0 - 74.5	0.35 - 2.75	0.65 b	0.04	***	0.71	14.5	3.9
Elattostachys apetala	19	5.0 - 12.5	0.15 - 1.10	1.10 ab	0.4	*	0.31	15.2	7.1
Fagraea berteroana	11	5.0 - 52.0	0.40 - 1.70	0.49 b	0.05	***	0.90	15.4	5.3
Ficus habrophylla	10	5.0 - 16.7	0.35 - 1.40	1.02 ab	0.29	*	0.49	16.2	5.6
Geissois racemosa	61	5.0 - 45.5	0.35 - 2.60	0.43 b	0.05	***	0.55	20.8	9.5
Guioa villosa	49	5.0 - 18.0	0.10 - 1.60	1.64 a	0.17	***	0.45	9.3	4.7
Melaleuca quinquenervia	46	5.0 - 28.1	0.40 - 2.05	0.35 b	0.11	***	0.25	20.4	9.1
Pittosporum simsonii	25	5.3 - 22.5	0.35 - 1.20	0.45 b	0.17	*	0.20	15.4	6.2
Tabernaemontana cerifera	21	5.0 - 20.2	0.55 - 1.80	0.69 b	0.08	***	0.72	22.9	4.3

"*", $P < 0.05$; "**", $P < 0.01$; "***", $P < 0.001$

6.5.2 Bark thickness and bole cambium injuries

The 11 species had very contrasting capacity to avoid injuries on bole cambium induced by fire due to differences in bark investment patterns (Table 6.5). *Geissois racemosa, Melaleuca quinquenervia* and *Tabernaemontana cerifera* showed high investment in bark and thus high capacity to avoid fire injuries on bole cambium while conversely, *Achronychia laevis* and *Guioa villosa* were likely very vulnerable to these injuries.

Allometric relationships between BT and DBH were significant for all species and showed 3 different patterns of bark thickness increment related to different bark allometric coefficient (α_{BT}, see Table 6.5); *Acronychia laevis* and *Guioa villosa* showed positive allometry ($\alpha_{BT} > 1$, concave form), *Elattostachys apetala* and *Ficus habrophylla* showed isometric allometry ($\alpha_{BT} \sim 1$, upward form) while most of the studied species (*Alstonia costata, Codia albicans, Fagraea berteoroana, Geissois racemosa, Melaleuca quinquenervia, Tabernaemontana cerifera and Pittosporum simsonii*) showed negative allometry ($\alpha_{BT} < 1$, convex form). Bark thickness were equivalent to 15.8 % (± 4.3 SD) of the stem radius on average and ranged from 8.1 % (± 2.5 SD) to 22.9 % (± 4.3 SD) for *Alstonia costata* and *Tabernaemontana cerifera*, respectively.

Normalized bark thickness (NBT, *i.e.* BT in percentage of the stem radius) tended to decrease with the estimated bark allometric coefficient (*i.e.* the lower is α_{BT}, the earlier is the investment in bark and the higher is the percentage of bark, see Figure 6.4), however the correlation was not significant (Spearman's rank test, P = 0.32 and P = 0.18 within taking account *Alstonia costata*). In a nutshell, the species located in the lower right part of the Figure 6.4 (*Acronychia laevis* and *Guioa villosa*) were likely the most vulnerable to cambial injuries whereas the species located in the upper left part (*Geissois racemosa*, *Melaleuca quinquenervia* and *Tabernaemontana cerifera*) were likely more protected to cambial injuries.

In the range of the studied DBH, and for fire with a 1 min residence time, only *Acronychia laevis, Guioa villosa* and *Elattostachys apetala* had too thin bark (BT < 1.15 cm) to avoid bole cambium injuries with a fire of 1000 $kW.m^{-1}$ (Figure 6.5). This was due to both low investment in bark (low NBT and high α_{BT}) and low DBH, even

through the real range of DBH is likely higher for *Elattostachys apetala* than the studied range. The range of minimum DBH required for the others species to avoid cambium injuries during such fire was quite important from *ca* 11 cm for *Tabernaemonatana cerifera* to *ca* 42 cm for *Alstonia costata*, respectively. *Geissois racemosa*, *Melaleuca quinquenervia* and *Tabernaemontana cerifera* showed particularly high capacity to avoid bole cambium injuries as they likely could quickly reach the minimum DBH required to avoid fire of 1000 $kW.m^{-1}$ (12.2, 13.9 and 11.1 cm, respectively), 2500 $kW.m^{-1}$ (17.6, 21.0 and 14.2 cm, respectively) or 5000 $kW.m^{-1}$ (23.3, *ca* 30 and 17.2 cm, respectively). Moreover, *Codia albicans* and *Ficus habrophylla* could also avoid these fires, however their minimum required DBH were noticeably higher (*e.g.* 18.6 and 20.4 cm for I = 1000 $kW.m^{-1}$).

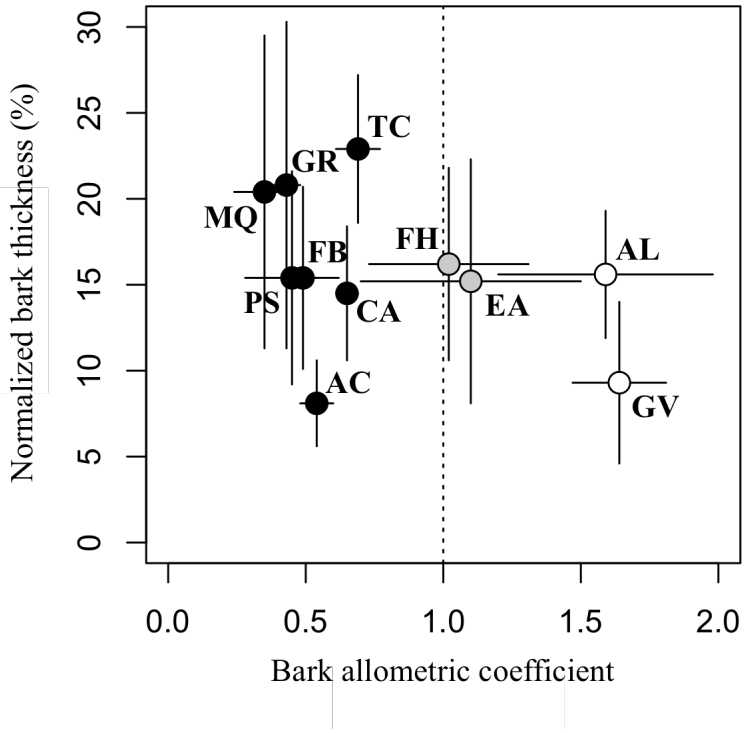

Figure 6.4 *Normalized bark thickness against bark allometric coefficients (bars represent one standard-error). The two-letter codes refer to species (see* Table 6.1*).*

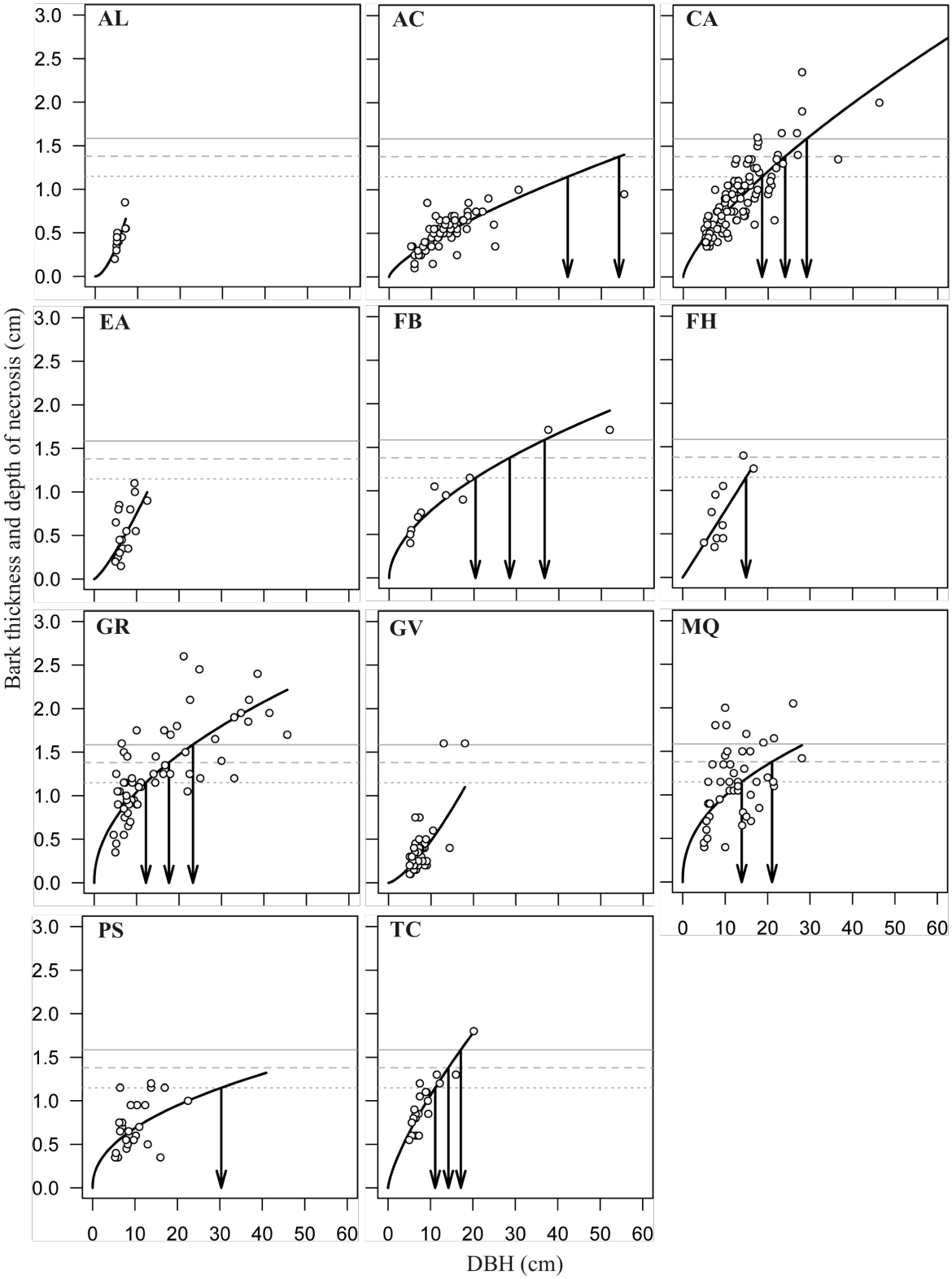
AL
AC
CA
EA
FB
FH
GR
GV
MQ
PS
TC
Bark thickness and depth of necrosis (cm)
DBH (cm)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
0
10
20
30
40
50
60

Figure 6.5 (previous page) *Specific allometric relationships between bark thickness and stem diameter at breast height (DBH). The two-letter codes refer to species (see Table 1), grey horizontal lines represent the estimated depth of necrosis for a fire of 1 min residence time and I = 1000, 2500 or 5000 kW.m^{-1} and arrows show the minimum DBH required to avoid bole cambium injuries. All represented relationships are significant (P < 0.05).*

6.5.3 Tree height and crown injuries

The studied species encompassing trees and small trees had overall low tree height (TH) and tree crown base height (CBH) growth and thus were very exposed to scorching and associated crown injuries even for low intensity fires.

Allometric coefficients for TH growth (α_{TH}) were significant for all studied species (P < 0.05, see Table 6.6) but more surprisingly α_{TH} were of the same order for trees (from 0.46 ± 0.04 SD for *Codia albicans* to 0.64 ± 0.03 SD for *Geissois racemosa*) and small trees (from 0.40 ± 0.15 SD for *Fagraea berteoroana* to 0.47 ± 0.09 SD for *Acronychia laevis*). However, relationships between CBH and DBH were weaker and only six species showed significant α_{CBH} (4 among the 5 trees and only 1 among the 6 small-trees species). Given that, as suggested above by the analysis of covariance (see Table 6.4) CBH were likely more determined by environmental (*e.g.* fires, grazing, competition with other trees or grasses) than by ontogenetic factors. Only *Geissois racemosa* and *Melaleuca quinquenervia* showed high significant relationships between CBH and DBH suggesting an important ontogenetic determinism of CBH.

In the range of the studied DBH, most of the small-trees were likely totally scorched for low intensity fires (*i.e.* I = 1000 kW.m^{-1}, potential scorch height ≈ 6 m) while for trees the minimum DBH required to preserve half of the tree from scorch ranged considerably, from 10.6 cm for *Alstonia costata* to 25.4 cm for *Melaleuca quinquenervia* (Figure 6.6). However, all of these last-one were likely totally scorch for I = 5000 kW.m^{-1} (*i.e.* potential scorch height ≈ 17 m).

Table 6.6 *Estimated allometric coefficient (α) for the DBH-tree height (TH) and DBH-tree crown base height (CBH) relationships.*

Species	Traits	N	DBH range (cm)	Height range (m)	Height α			
					Estimate	SE	P	R^2
Acronychia laevis	TH	27	1.2 - 7.2	1.6 - 6.8	0.57	0.09	***	0.61
	CBH	-	-	1.0 - 3.1	0.29	0.13	*	0.13
Alstonia costata	TH	10	3.0 - 18.7	4.0 - 15.7	0.60	0.07	***	0.90
	CBH	-	-	2.6 - 5.5	ns.	ns.	ns.	0.18
Codia albicans	TH	178	4.7 - 43.0	3.3 - 13.0	0.46	0.04	***	0.44
	CBH	25	5.0 - 36.5	1.7 - 8.9	0.50	0.19	*	0.19
Elattostachys apetala	TH	35	1.2 - 12.5	2.0 - 8.7	0.55	0.06	***	0.69
	CBH	33	-	1.4- 4.6	0.34	0.09	**	0.27
Fagraea berteroana	TH	14	5.5 - 22.5	4.4 - 13.6	0.40	0.15	*	0.31
	CBH	3	19.0 - 22.5	1.4 - 4.3	ns.	ns.	ns.	-0.32
Ficus habrophylla	TH	13	2.0 - 16.7	2.6 - 7.6	0.42	0.10	**	0.56
	CBH	-	-	1.1 - 4.7	ns.	ns.	ns.	-0.09
Geissois racemosa	TH	106	1.1 - 38.5	1.6 - 18.7	0.64	0.03	***	0.84
	CBH	70	-	1.1 - 9.4	0.35	0.06	***	0.32
Guioa villosa	TH	140	1.0 - 18.0	2.3 - 11.1	0.50	0.04	***	0.51
	CBH	52	1.0 - 14.4	1.0 - 4.5	ns.	ns.	ns.	-0.01
Melaleuca quinquenervia	TH	211	2.0 - 28.1	2.0 - 10.6	0.54	0.03	***	0.57
	CBH	207	-	1.1 - 6.2	0.41	0.05	***	0.28
Pittosporum simsonii	TH	98	1.0 - 40.9	1.7 - 19.1	0.62	0.02	***	0.86
	CBH	33	1.0 - 13.8	1.0 - 6.7	0.24	0.07	**	0.27
Tabernaemontana cerifera	TH	38	1.5 - 16.0	1.7 - 7.2	0.57	0.05	***	0.75
	CBH	37	-	0.6 - 2.5	0.24	0.10	*	0.12

"*", $P < 0.05$; "**", $P < 0.01$; "***", $P < 0.001$

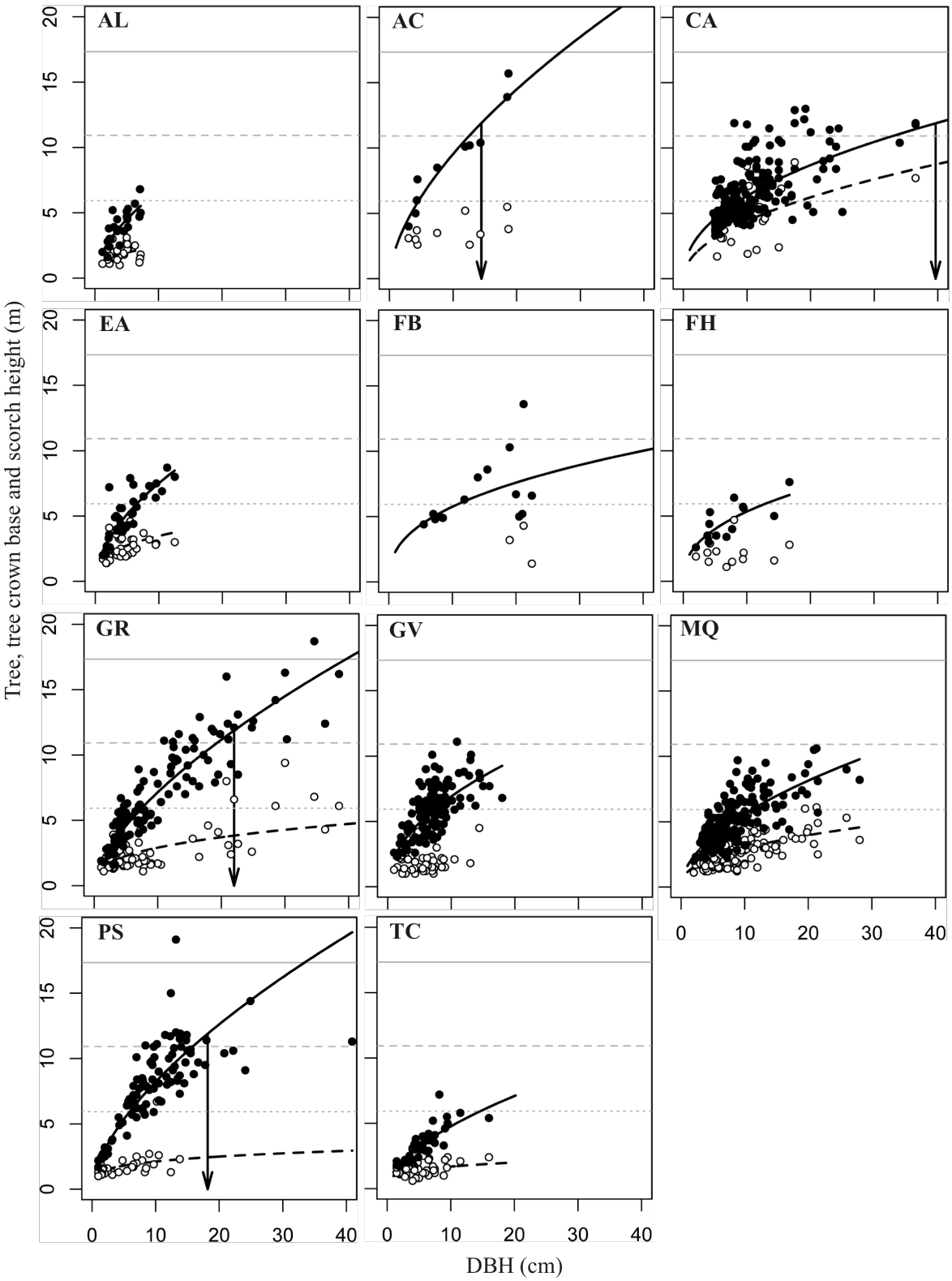
AL
AC
CA
EA
FB
FH
GR
GV
MQ
PS
TC
Tree, tree crown base and scorch height (m)
DBH (cm)
0
5
10
15
20
0
10
20
30
40

Figure 6.6 (previous page) *Specific allometric relationships between tree height (black circles and full lines) and tree canopy base height (white circles and dotted lines) against stem diameters at breast height (DBH). The two-letter codes refer to species (see Table 1), grey horizontal lines represent estimated scorch height for a fires of I = 1000, 2500 or 5000 kW.m^{-1} and arrows show the minimum DBH required to prevent the half of the tree from scorch (for I = 1000 kW.m^{-1}). All represented relationships are significant (P < 0.05).*

6.6 Discussion

6.6.1 Bark thickness, not tree height, differentiate species fire tolerance

We compared fire resistance (or avoidance) traits of early secondary successional species growing in fire prone savannas. In such ecosystem, trees and small-trees must quickly develop defences to avoid fire injuries and stem mortality (top-kill) in order to recruit into the adult population (Jackson et al. 1999). From a morphological point of view, two main defence strategies have been described in the literature: (i) to grow in height to raise apical buds above the flame height (e.g. Bond 2008; Higgins *et al.* 2000) or / and (ii) to grow in width and develop thick bark to protect the cambium from fire (e.g. Hoffmann *et al.* 2003; Pinard and Huffman 1997).

The studied species did not present sufficient growth in stem and canopy heights to raise their apical buds above flames and scorch height, even for low-intensity fire which are common in NC savannas. While these species did not show contrasting response to scorching, they showed contrasting responses to bole heating due to differences in bark thickness increments. This supports the idea that interspecific variation in fire response will be explained by variation in bark thickness and stem diameter (Balfour and Midgley 2006), which are positively correlated together (e.g. Hoffmann *et al.* 2009; Hoffmann *et al.* 2003; Jackson *et al.* 1999).

Bark thickness is likely the most important morphological characteristic that affects top-kill. Whelan (1995) and more recently Lawes *et al.* (2011) suggest that growing in height is of no advantage if the cambium is not protected in the stem.

Moreover, Balfour and Midgley (2006) experimentally showed for an African *Acacia* species that death of the canopy buds is not sufficient to cause top-kill. Thus, optimising bark thickness is likely the only strategy for avoiding top-kill in fire prone savannas (Lawes et al. 2011).

Table 6.7 *Resprouting capacity (+ for able to resprout, - for not able to resprout and ? for not observed)*

Species	Resprouting ability		References
	Root-sprouting	Shoot-spouting	
Acronychia laevis	+	-	This study
Alstonia costata	?	?	
Codia albicans	+	?	This study
Elattostachys apetala	+	?	Boquet *et al.* 2007
Fagraea berteroana	?	?	
Ficus habrophylla	?	?	
Geissois racemosa	+	+	This study
Guioa villosa	+	-	This study ; Jaffré *et al.* 1997
Melaleuca quinquenervia	+	+	
Pittosporum simsonii	?	?	
Tabernaemontana cerifera	+	+	This study

Resprouting is an alternative to fire resistance that allow individuals to persist after a fire, and it likely allows trees and grass to coexist in savannas (see Higgins *et al.* 2000; Vesk 2006). Many woody species can resprout and many ecosystems(particularly fire-prone ones) are dominated by resprouters (Bond and Midgley 2001). Regarding the studied species, even if there are few data on resprouting capacity (see Table 6.7 for review), most of these are also likely able to resprout from the roots after-fire. The resprouting of juveniles allows species to persist in fire prone ecosystems and the recruitment into the mature size depends on rare opportunities, to reach the escape size (Archibald and Bond 2003; Higgins *et al.* 2000; Vesk 2006). Thus, the quicker juveniles develop defences such as bark, the quicker they reach the escape size and the higher are theirs opportunities to recruit in the mature size.

6.6.2 New Caledonian "savannas species" poorly adapted to savannas fire regime

One of our most striking results is that the early secondary successional species growing in New Caledonian savannas were relatively poorly adapted to fire from a bark point of view. Although most of them invested disproportionally more in bark at small DBH, which is typical of savannas species (Jackson et al. 1999), their investment in bark was sensibly lower than species in others savannas worldwide. Indeed, in comparison with the results from Brazilian Cerrado (Hoffmann *et al.* 2003), the average NBT of NC species (15.3 %) is closer to that of forest species than to savannas ones (10.1 and 28.5 %, respectively). Moreover, in comparison with the results from northern Australia (Lawes et al. 2011), the NBT of NC species is more than twice smaller than species of savannas (34.0 %).

Functional explanations for the variation in BT are not clear (Paine et al. 2010). Giving the important role of bark in protecting stem to fire heat, it is however clear that frequent and sufficiently intense fires impose a substantial selection pressure on BT (Midgley *et al.* 2010; Stephens and Libby 2006). For example, savannas species submitted to high frequency of relatively intense fire present thicker bark than forest species submitted to lower fire frequency and intensity (Hoffmann *et al.* 2003).

In New Caledonia, savannas and maquis (which is a low, sclerophyllous, evergreen, heath-like formation largely restricted to ultramafic substrates, Lowry II 1998) are the two main fire prone ecosystems (Jaffré *et al.* 1998; McCoy *et al.* 1999). These two contrasting ecosystems had both widely expanded at the expense of forest since the settlement of Humans on the island (*ca* 3000 years ago) and the anthropogenic increase of fire frequency (Jaffré *et al.* 1998; Stevenson 2004). However, according to paleoecological records, savannas likely appeared for the first time when Humans settled in NC (Stevenson 2004) whereas maquis and forest-maquis dynamics driven by climate variations and natural fires existed long before (Hope and Pask 1998; Stevenson and Hope 2005). Thus, Jaffré *et al.* (1997b) suggest that species growing in maquis are well adapted to fire as a result of long-term adaptation. However, according to McCoy *et al.* (1999) although maquis species tolerate fire thought theirs rootstocks (which is not exclusive to fire tolerance) that allow them to resprout after fire, they do not show others fire adaptations such as thick bark or epicormic regrowth. In contrast with

maquis and given the relatively recent existence of savannas in NC, we hypothesise that fire pressure is too recent to have substantially selected a set of species well adapted to the dramatically increased savanna fire regime since *ca* 3000 years.

6.6.3 Implications for rainforest-savanna dynamics and management

Since the settlement of Humans in New Caledonia, savannas had widely expanded at the expense of forest (see Jaffré et al. 1998). The maintaining of a diversity of ecosystems in the New Caledonian landscape such as forest-savanna mosaic support the biodiversity (Jaffré 1993). It is worldwide recognized that fire and fire regime diversity may support biodiversity (Driscoll et al. 2010), however in New Caledonia socio-environmental changes such as dramatic increase of invasive weeds and mammals or fire practices modification likely modify fire regime and threaten biodiversity and ecosystems services. In this context, restoration and fire management may be two complementary ways to manage landscape by both promoting secondary succession and limiting forest erosion, and preserving a landscape mosaic.

Species that are resilient to fire and can avoid top-kill are clearly advantaged in fire-prone savanna (Lawes et al. 2011). In most of the New Caledonian savannas, *Melaleuca quinquenervia* is the only woody species. Indeed, this species although originally growing in swampy areas is very tolerant to savanna fires, encompassing morphological defence such as thick multi-layers spongy bark, high resprouting capacity from roots and shoots (from epicormic buds) and high fire-induced seed release (Serbesoff-King 2003). However, savannas could be colonised by early secondary successional species when fire frequency and / or intensity decrease (see Ibanez et al. submitted). Among these species, *Geissois racemosa* and *Tabernaemontana cerifera* presented bark increment patterns and thickness close to those of *Melaleuca quinquenervia* ones. In comparison with the others, *Geissois racemosa* is frequently observed as adult isolated trees in savannas (Ibanez et al. submitted) suggesting that it is more tolerant to fire. The fire scars observed on *Geissois racemosa* individuals support this hypothesis. These isolated trees that could increase seed rain by perch effect and promote secondary succession (Rigg *et al.* 2002; Toh *et al.* 1999) make *Geissois racemosa* an interesting candidate for forest restoration.

Decrease in fire frequency (*e.g.* by fire prevention and fighting) to allow species to constitute their defences, and / or decrease fire intensity (*e.g.* by removing grasses, clearing shrubs and prescribed fire) to decrease fire severity and top-kill may be two alternative to promote the installation of mature trees in savannas but also to protect surrounding forest from fire injuries. The fight against invasive weeds, such *Lantana camara* and *Melinis minutiflora* that often dominate the New Caledonian savanna ground layer and likely modify fire regime and severity (see Brooks *et al.* 2004; Dantonio and Vitousek 1992; Hoffmann *et al.* 2004) may be a way to manage fire regime. It should be noted that the decrease in fire frequency can lead to fuel accumulation and finally to more intense and severe fires, while early dry season fires would limit the occurrence of intense fires at late dry season and thus dramatically decrease fire intensity and severity (Govender *et al.* 2006; Murphy and Russell-Smith 2010; Williams *et al.* 1998). At the landscape scale, fire regime diversity so-called pyrodiversity may begets biodiversity (see Parr and Andersen 2006).

6.7 Acknowledgements

We thank the ANR BDIV-07-008 project INC and the CNRS for funding this research and the PhD scholarship of T. Ibanez. We are grateful to Hubert Géraux and the WWF for logistic and to Denis Meandu-Poveu for a great and enthusiastic help in the field. We also thank Jérôme Munzinger, Philippe Birnbaum and Vincent Bonhome for their useful comments on earlier version of the manuscript.

6.8 Appendix

Description of the fuels / vegetations scenarios used for BehavePlus fire simulation.

Savannas	Surface / Understory - fuel / vegetation load (tonne/ha)					Fuel bed depth	Overstory - fuel / vegetation		
	1-h	10-h	100-h	Live herbaceous	Live Woody	(m)	Canopy cover (%)	Canopy height (m)	Canopy base height (m)
1	0.00	0.61	0.56	3.14	0.00	0.40	38.25	6.40	2.72
2	3.13	1.08	1.12	3.18	1.30	0.57	42.45	6.71	2.21
3	5.58	0.73	0.56	8.60	0.00	1.07	45.75	7.94	2.52
4	1.41	0.81	0.44	5.20	6.98	0.48	35.45	11.64	2.45
5	1.75	1.70	2.47	9.59	0.00	0.54	48.80	6.01	2.03
6	1.15	1.40	0.00	6.81	0.21	0.57	45.40	6.22	4.64
7	2.98	1.21	0.59	12.66	0.42	0.49	47.00	6.80	4.65
8	1.91	1.05	0.33	15.73	1.01	0.54	52.00	7.14	1.72
9	2.41	0.85	0.67	6.97	0.20	0.29	23.10	6.64	2.02
10	6.45	0.77	1.94	25.10	0.00	0.97	41.00	6.93	2.10
11	1.99	1.65	0.63	8.39	3.13	0.59	70.50	3.87	1.08
12	1.98	1.08	1.28	15.02	0.83	0.53	36.10	7.78	2.75
13	2.53	1.46	1.25	18.52	0.00	0.58	39.10	7.40	2.41

14	6.47	0.98	2.44	13.62	0.00	0.74	34.30	5.41	1.51
15	5.41	0.56	0.34	13.59	0.55	0.78	11.20	5.15	1.65
16	3.56	1.15	0.11	15.93	1.76	0.67	40.00	7.66	1.95
17	3.81	1.16	1.25	14.83	1.57	0.65	40.00	8.09	2.62
18	10.99	2.33	2.02	2.38	0.30	0.66	67.80	9.21	2.69
19	1.60	0.17	0.67	0.86	0.54	0.13	22.00	6.73	1.63
20	4.80	2.35	0.67	0.11	1.55	0.24	46.80	5.33	2.06
21	8.11	0.84	1.34	1.22	0.40	0.51	47.80	6.74	3.26
22	1.36	1.96	0.00	5.50	2.51	0.74	2.80	2.80	0.60
23	0.55	1.33	0.68	4.04	0.00	0.32	32.00	6.83	3.70
24	5.83	0.19	0.00	2.61	0.00	0.31	42.80	11.00	6.50
25	0.48	1.05	1.82	2.55	0.00	0.36	45.40	7.42	2.85
26	0.00	0.56	0.00	4.58	0.00	0.40	5.00	8.00	4.00
27	6.10	0.96	1.67	15.25	0.45	0.66	18.40	6.33	2.50
28	3.41	0.75	0.00	6.52	1.00	0.48	17.80	5.60	0.30
29	5.53	2.45	2.40	3.12	0.00	0.43	63.20	7.14	2.44
Mean	3.49	1.14	0.94	8.66	0.87	0.54	38.01	6.93	2.54
Minimum	0.00	0.17	0.00	0.11	0.00	0.13	2.80	2.80	0.30
Maximum	10.99	2.45	2.47	25.10	6.98	1.07	70.50	11.64	6.50

7 Note on *Melaleuca quinquenervia* population dynamics and fire

This section presents preliminary results as supplementary material, which will not be submitted for publication.

7.1 Introduction

Melaleuca quinquenervia (Cav.) S.T. Blake (*Myrtaceae*), known as the broad-leaved paperbark tree, is native from Australia, New Caledonia and Papua New Guinea but occurs into others tropical and sub-tropical countries in Oceania, Asia, western Africa and southern North America (Serbesoff-King 2003; Watt *et al.* 2009). *M. quinquenervia* is a problematic species in many countries, it is considered as (i) widely invasive in Florida (Dray *et al.* 2006; Serbesoff-King 2003), (ii) moderate invasive in Hawaii (Sherley 2000), Puerto Rico (Pratt *et al.* 2005) and in the US territory of Guam (Sherley 2000) and (iii) potential invader in Micronesia (Sherley 2000) and in Hong Kong (see Serbesoff-King 2003 and Watt *et al.* 2009 for more references).

Owing to the invasive status of *M. quinquenervia* in Florida, a great literature on its ecology in this country has been developed (e.g. Lopez-Zamora *et al.* 2004; Myers 1983; Rayamajhi *et al.* 2002; Serbesoff-King 2003; Turner *et al.* 1998; Van *et al.* 2005). There is also a substantial literature on its ecology in Australia, particularly in comparison with its ecology in Florida (Rayamajhi *et al.* 2002; Turner *et al.* 1998). Conversely the ecology of *M. quinquenervia* in New Caledonia and Papua New Guinea had to our knowledge retained less interest.

In New Caledonia, although *M. quinquenervia* (locally known as “niaouli”) is a native species (Jaffré *et al.* 2001) its current distribution has widely overcome its natural distribution leading some authors to consider it as an invasive species (e.g. Mittermeier *et al.* 2004). Indeed, paleoecological records suggest that *M. quinquenervia*, which dominates the New Caledonian savannas today (more than 30 % of the main island) was restricted to swampy areas before human colonization 3500 years ago (Stevenson 2004).

M. quinquenervia widely dominates the New Caledonian savannas and is often the only woody species remaining in frequently burned savannas (pers. obs.). Savanna fires often totally burn the grass layer leaving a bare-soil, while *M. quinquenervia* persists, limiting therefore soil erosion. Soil retention is a critical ecosystem service for water supply and lagoon conservation, especially because of New Caledonia presents hilly landscapes submitted to high rainfalls, and coral reefs threatened by sedimentation (Roberts *et al.* 2002). However, as showed by Liedloff and Cook (2007) for *Eucalyptus*

spp. in Australia, although *M. quinquenervia* is a fire tolerant species (Serbesoff-King 2003), its populations are likely affected by fire regime.

In this note, we proposed a first post-fire mortality analysis of *M. quinquenervia* in New Caledonian savannas.

7.2 Methods

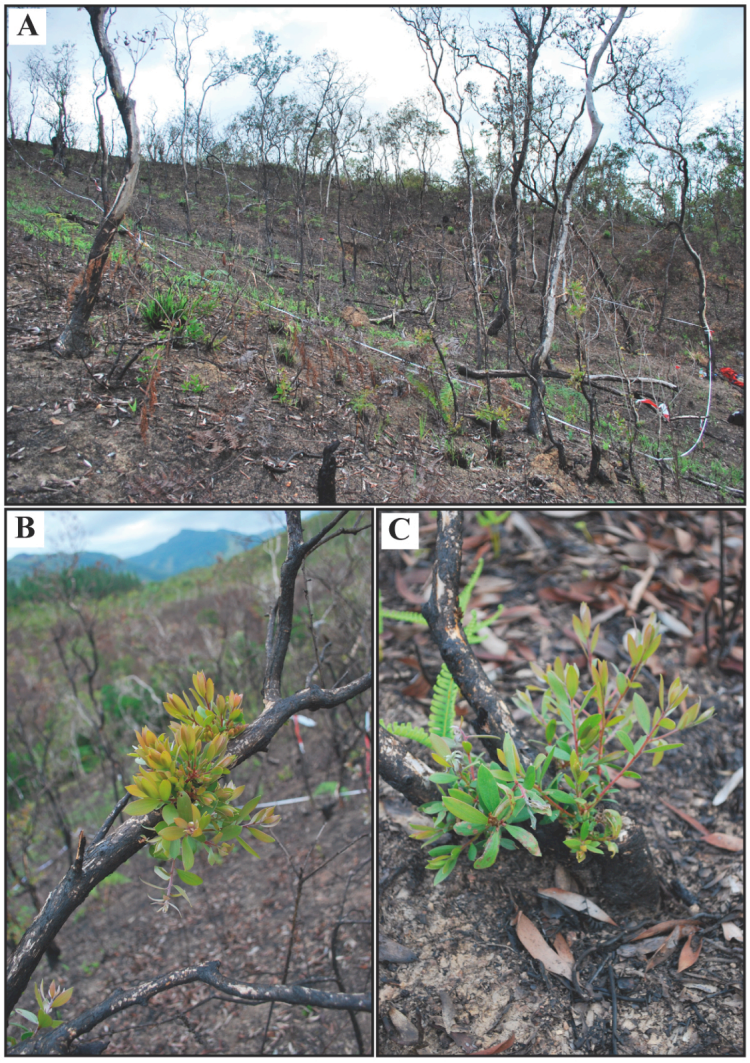

Figure 7.1 *Photographs of burned M. quinquenervia savannas. (A) Sample design. M. quinquenervia resprouting from epicormic buds along a branch (B) and at the base (C).*

We assessed post-fire mortality of *M. quinquenervia* trees and seedlings (*i.e.* < 2 m height) in five sites ranging from 100 to 300 m^2 for a total of 1000 m^2 (Table 7.1 and Figure 7.1.A). The studied sites were located in savannas surrounding the *Gohapin* tribe (see Ibanez *et al.* submitted-b for more details on the study area). The sampling was done during the late dry season (from November 13th to December 22nd, 2009) few months after the fires, which occurred sooner in the dry season. Unfortunately, we don't have precise data about the fires (intensity, rate of spread, flame height) that burned these sites, nevertheless, at the moments of the samples, the grass layer was totally burned and the trees were totally or partially scorched (see Ibanez *et al.* submitted-a for more information on potential fire characteristics in New Caledonian savannas).

In the studied sites, seedling and tree densities ranged from 19.0 to 113.5 stems.100 m^{-2} and from 10.3 to 33.0 stems.100 m^{-2}, respectively (62.7 and 16.9 in average). We confronted post-fire survival (*i.e.* post-fire resprout from the base or from the stems, see Figure 7.1.B-C, respectively) to seedlings and trees (*i.e.* height $\geq$ 2 m) characteristics: diameter at the base, height and reproductive maturity (*i.e.* presence of capsules along the stems or not) for seedlings, and diameter at breast height (DBH), height and the crown base height for trees.

7.3 Results and discussion

The most striking result was that although the proportion of resprouting seedlings and trees varied significantly according to the different sites (Fig. 2), most of the seedlings (59.2 %) and trees (71.0 %) resprouted after fire. This high resprouting capacity is likely due to both the high increment pattern (Ibanez *et al.* submitted-a) and the high insulating capacity (Serbesoff-King 2003) of its bark, which protect its cambium, but also to the presence of epicormic buds (Serbesoff-King 2003).

Surprisingly, the measured seedlings and trees characteristics poorly explained (3.8 and 4.3 %, respectively) the variability observed in resprouting (Table 2). Another result to note was that seedlings reached quickly their maturity, indeed 17 % of the inventoried seedlings were mature and we inventoried 10 cm height seedlings that were already mature.

Table 7.1 *Sampling description (Dim. for dimension, Nb. For number and BA for basal area).*

Site	Dim. (m)	Area (m^2)	Slope (%)	Seedlings		Trees		
				Nb. of stems	Density (stems / 100 m^2)	Nb. of stems	Density (stems / 100 m^2)	BA (m^2 / 100 m^2)
1	10*10	100	43.7	105	105.0	33	33.0	2.1
2	10*30	300	52.0	206	69.0	31	10.3	0.4
3	10*20	200	38.7	52	26.0	31	15.5	0.9
4	20*10	200	48.8	37	19.0	40	20.0	0.6
5	20*10	200	27.5	227	113.5	34	17.0	0.7
Total		1000	42.1	627	62.7	169	16.9	0.9

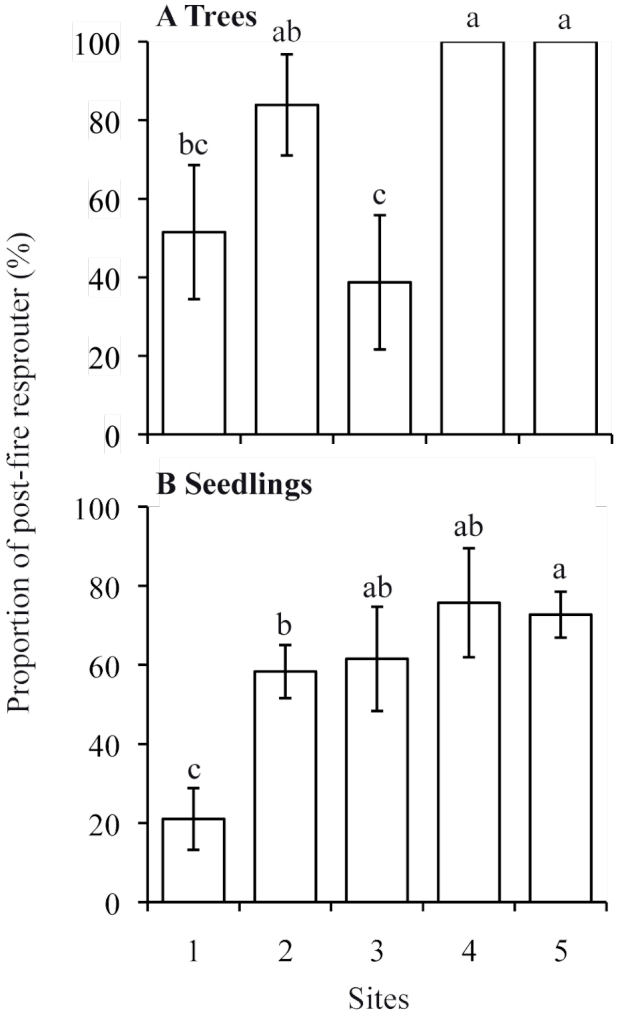

Figure 7.2 *Proportion of post-fire resprouter in the different sites. Letters show significant difference between proportion using the Marascuillo procedure for multiple comparison with a level of significance of 0.05.*

Table 7.2 *Analysis of co-variance of seedlings and trees resprouting*

Seedlings	Sum Sq.	Var. explained (%)	Df	F value	P
Stem height	26.52	3.8	1	26.3188	***
Diameter at the base	0.32	0.0	1	0.3180	
Stem maturity	0.09	0.0	1	0.0887	
Site	74.18	10.3	4	18.4570	***
Residuals	615.61	85.9	611	-	-
Trees					
DBH	6.379	3.5	1	6.7058	*
Tree height	0.283	0.2	1	0.2970	
Crown base height	1.295	0.6	1	1.3616	
Site	52.356	28.8	4	13.7600	***
Residuals	121.757	66.9	128	-	-

"*", $P < 0.05$; "**", $P < 0.01$; "***", $P < 0.001$

Our preliminary results confirmed the capacity of *M. quinquenervia* to survive to fire. However, more studies are needed to evaluate the impact of different fire regimes (frequency and intensity) and stand conditions (*e.g.* water availability) on *M. quinquenervia* populations. Such data, combined to population dynamic models, such as FLAME (Liedloff and Cook 2007), would provide a good framework to test the impacts of different fire management scenarios on *M. quinquenervia* populations and associated ecosystems services.

Finally, we suggest that owing to the particular biogeography history of *M. quinquenervia* and its wide range of distribution (spreads on 6000 km2 to 700 m asl high Jaffré *et al.* 2009), studying its ecology in New Caledonia could provides critical information to predict its worldwide potential distribution (see Watt *et al.* 2009).

8 Low seed-rain but enhanced by perch effect in a New Caledonian savanna

This section is in preparation for submition to *Restoration Ecology* as the following research paper :

Ibanez, T., Géraux, H., and Hély, C., (in prep.). Low seed-rain but enhanced by perch effect in a New Caledonian savanna, in preparation for submition to *Restoration Ecology*.

8.1 Résumé

Le manque de graines peut limiter l'établissement d'arbres et le retour de la forêt dans les zones ouvertes. La dispersion des graines par les oiseaux dans ces zones telles que les savanes est affectée à différentes échelles spatiales par la structure du paysage et celle de la zone ouverte elle-même. Des perchoirs artificiels ou naturels tels que les arbres peuvent attirer les oiseaux et augmenter l'arrivée des graines. Dans cette étude, nous avons testé l'hypothèse selon laquelle l'établissement d'arbres pionnier dans la savane peut favoriser l'arrivée de graines par effet perchoir. Pour cela, nous avons comparé l'arrivée de graines recueillies par des pièges placés sous quatre traitements: l'arbre dominant de savane, *Melaleuca quinquenervia*, deux espèces d'arbres pionniers *Geissois racemosa* et *Pittosporum simsonii* et dans les zones sans couverts (contrôle sans arbres). Le faible nombre de graines récoltées met en évidence la nécessité d'artificiellement augmenter la pluie de graines ou de planter des directement des plants pour restaurer la forêt dans les écosystèmes très fragmenté. Nos résultats suggèrent que des espèces pionnières tels que *Geissois racemosa* peuvent augmenter la pluie de graines dispersées par les oiseaux. Cependant à la vue des résultats, des études portant sur des arbres potentiellement plus attractifs sont nécessaires afin optimiser les efforts de restauration forestière.

Mots-clés: attractivité des arbres; dispersion; oiseaux; ornithochore; pièges à graines ; restauration forestière.

8.2 Abstract

The lack of seeds arrival can limit tree recruitment and the recovery of forest in open areas. The dispersal of seeds in an open areas such as savanna by birds is affected at different spatial scales by both the landscape structure and the structure of the open area itself. Artificial perches or natural ones such as trees may attract birds and enhance seed arrival. In this study, we tested the hypothesis that the establishment of early pioneer tree in savanna may increase seed arrival because of perch effect. For this, we compared seed arrivals collected by seed-traps placed under four treatments: the savanna dominant tree species, *Melaleuca quinquenervia*, two pioneer tree species *Geissois racemosa* and *Pittosporum simsonii* and in open savanna areas (control with no trees). The low arrivals of seeds highlight the need for artificially increasing seed-rain or adding seedlings to restore forest in highly fragmented ecosystems. Our results suggest that planting early secondary species such as *Geissois racemosa* may increase bird-dispersed seed rain. However, studies on potentially more attractive trees were needs to optimise forest restoration.

Keywords: birds; dispersal; forest restoration; ornithocorous; tree attractiveness; seed traps.

8.3 Introduction

Seed dispersal is a critical process that affects the structure and dynamics of plant populations and communities (Clark et al. 1999; Nathan and Muller-Landau 2000). Since the lack of seeds arrival can limit tree recruitment and the recovery of forest in degraded open area, measuring and understanding the arrival of seeds have strong implications for forest restoration (Holl 1999; Zimmerman et al. 2000). While the arrival of wind-dispersed seeds mainly depends on the distance from the seeds sources, the arrival of animal-dispersed seeds such as bird-dispersed seeds also depends on behaviours of dispersers (Muller-Landau et al. 2008). The dispersal of seeds in an open area by birds – which are worldwide important dispersers (Sekercioglu 2006; Whelan et al. 2008) – is affected at different spatial scales by both the landscape structure (*e.g.* Herrera and Garcia 2010; Levey et al. 2005) and the structure of the open area itself (*e.g.* Fink et al. 2009; McDonnell and Stiles 1983; Medellin and Gaona 1999).

In open areas, artificial perches (*e.g.* Holl 1998; McDonnell and Stiles 1983; Shiels and Walker 2003) or natural ones such as trees (*e.g.* Guevara et al. 1986; Holl et al. 2000; Slocum and Horvitz 2000) attract birds and enhance seeds arrival. The importance of this perch effect (*i.e.* the higher seed arrivals under the perch in comparison with open areas) depends on the attractiveness of the perch for birds (Fink et al. 2009; Slocum and Horvitz 2000). Perches such as isolated trees in open areas may provide recruitment foci (McDonnell and Stiles 1983) and promote forest recovery by nucleation processes (Reis et al. 2010; Schlawin and Zahawi 2008).

In the New Caledonian biodiversity hotspot (Mittermeier et al. 2004; Myers 1988) rainforest mainly replaced by anthropogenic formation – mainly savannas on volcano-sedimentary substratum (see Ibanez *et al.* submitted-b) and maquis on ultramafic ones (Perry and Enright 2002b) – is highly fragmented at low and middle elevation (Jaffré et al. 1998). Since more than 80 % and 70 % of the rainforest trees and small-trees are dispersed by birds (or bats) in New Caledonia on volcano sedimentary (Gailhbaud, unpublished data) and ultramafic substratum (Carpenter et al. 2003) studying seed dispersal by birds in open areas have strong implications for forest restoration.

The aim of this study is to measure and characterise bird-dispersed seed arrivals in savanna in a fragmented rainforest-savanna mosaic landscapes. We hypothesis that the establishment of early pioneer trees in savanna may promote nucleation processes by locally increasing seed arrival by perch effect. Thus we test both if perch effect increases seed arrival into savanna and if seed arrival varies under different tree species.

8.4 Materials and Methods

The study took place in the New Caledonian located in the south Pacific just above the Tropic of Capricorn (between 20°-23°S and 164°-167°E). The study area (400-500 m asl) was located in the middle of New Caledonia on the west side of the *Aoupinié* mountain (1006 m, 21°18' S, 165°27' E) in the *Gohapin* tribe (*ca* 20 km from the town of Poya). The landscape is a mosaic of remnant forests and wooded savannas shaped by recurrent fires (see Ibanez *et al.* submitted-b). The experimental device was placed within an area of forest restoration with 5 years of fire exclusion.

To test both if perch effect increases seed arrival into savanna and if seed arrival varies under different tree species, we compared seed arrival collected by seed-traps placed under four treatments: the savanna dominant tree species, *Melaleuca quinquenervia* (Cav.) S.T.Blake (Myrtaceae), two pioneer tree species *Geissois racemosa* Labill. (Cunoniaceae) and *Pittosporum simsonii* Montrouz. (Pittosporaceae) and in open savanna areas (control with no trees). *Geissois racemosa* is already used for forest restoration while *Pittosporum simsonii* is considered as a potential candidate (see Ibanez *et al.* submitted-c).

Melaleuca quinquenervia, locally known as Niaouli and *Geissois racemosa* both produces nectarous clustered flowers (white and red flowers, respectively) and dry fruits (woody capsules and siliques, respectively). However, *Melaleuca quinquenervia* has a sparse crown with small leaves (*ca* 5-10 cm long and 1-3 cm wide) while *Geissois racemosa* has a denser crown with large leaves (composed of 5 leaflets *ca* 5-20 cm long and 10-30 cm wide) offering greater shading. The *Pittosporum simsonii* crown presents intermediate characteristics with medium leaves (*ca* 1-10 cm long and 5-20 cm wide) and it produces little white clustered flowers and leathery dehiscent capsule.

We placed 20 seed-traps under each treatment for a total of 80 seed-traps distributed in seven sites in savanna near forest patches (Figure 8.1.A). When possible, we placed in the same sites (sites 1, 4 and 7) four seed-traps under each tree species and in the control open savanna. However, due to difficulty finding *Geissois racemosa* and *Pittosporum simsonii* in the same sites, we placed four seed-traps under *Geissois racemosa* and two under both *Melaleuca quinquenervia* and no trees in sites 2 and 5, and we did the same with *Pittosporum simsonii* in sites 3 and 6 (Table 8.1).

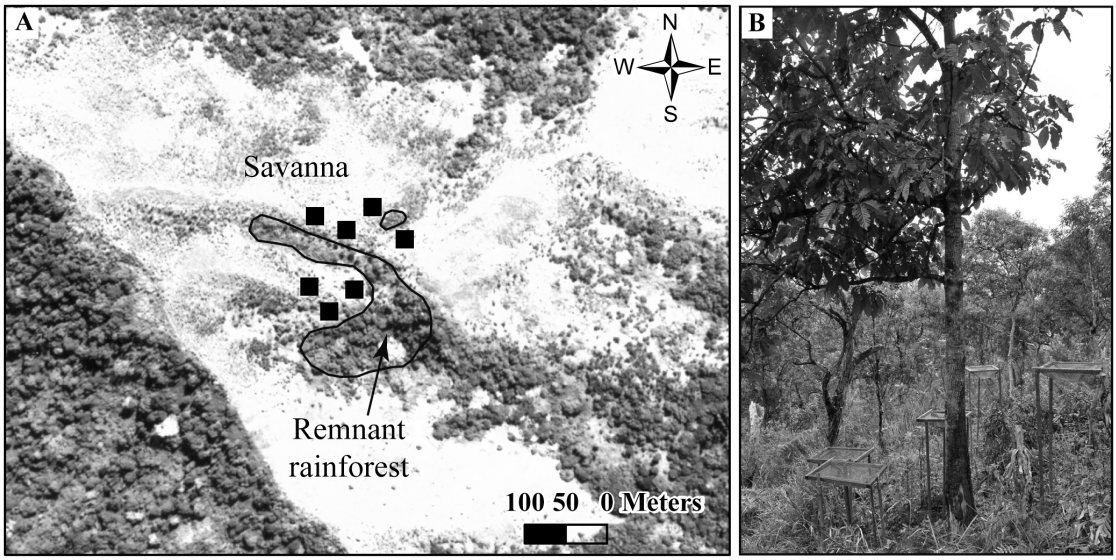

Figure 8.1 *Experimental design with A, location of both the seven sites (black squares) where seed-traps were placed and the inventoried forest fragments (black lines) and B, seed-traps placed under Geissois racemosa.*

Table 8.1 *Description of the experimental design. Number of seed-traps (tree) per treatments for each site.*

Treatments	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7
Melaleuca quinquenervia	4 (1)	2 (1)	2 (1)	4 (1)	4 (1)	2 (1)	2 (1)
Geissois racemosa	4 (1)	4 (1)	0 (0)	4 (1)	4 (1)	4 (1)	0 (0)
Pittosporum simsonii	4 (1)	0 (0)	4 (1)	4 (1)	4 (1)	0 (0)	4 (1)
No tree (control)	4 (1)	2 (1)	2 (1)	4 (1)	4 (1)	2 (1)	2 (1)
Total	16	8	8	16	16	8	8

The seed-traps used for seed collection (Figure 8.1.B) were 0.25 m^2 in area and were made of nylon mosquito netting (which drained water but kept seeds) stapled onto a wooden frame (0.5 m x 0.5 m). We stapled a steel grill (which let pass seeds) onto the other face of the seed-traps to protect the collected seeds from removal by rats, birds or others (see Cottrell 2004 about seed traps). Seed-traps were placed *ca* 1 m aboveground and *ca* 1.5 m far from the bole (see Figure 8.1.B) or randomly in open savannas. Seed traps were placed to collect seeds over one year between (from February 2010 to March 2011) with a fortnightly collect frequency except between February 9th 2010 and April 8th 2010 and between October 10th 2010 and February 11th 2011. Seed number and seed size defined through its length and width (*i.e.* the greater and second greater length, respectively) were measured to characterise the seed rain. Since our experimental design did not allow us to distinguish seeds dispersed by birds and bats we used the term birds for birds and bats throughout this manuscript.

In order to identify the collected seeds, we inventoried all trees with a diameter at breast height larger than 5 cm in forest fragments close to the sites (see Figure 8.1.A) and we constituted a seed bank reference. Seeds collected in the seed-traps were identified from both fresh material collected in these forest fragments and dry material from the herbarium of the centre IRD of Nouméa (NOU). We tested the effect of the treatment on seed abundance using analyses of variance on ranked data followed by multiple comparison Tukey HSD tests computed with R (R Development Core Team 2009).

8.5 Results

The abundance and the species richness of the seed rain were very low during the study period. Indeed, only 100 seeds coming from only 11 species (4 were not identified) were collected in the 80 seed-traps (Table 8.2). More than half of these seeds came from *Lantana camara* and *Psidium guajava* (45 and 19 %, respectively), which are invasive grass and shrub species, while the most represented non-invasive species were *Guioa villosa* and *Olea paniculata* (11 % each one). Seeds from 4 out of the 23 bird-dispersed species identified in the surrounding forest fragments were collected (see

Appendix). Overall, the collected seeds were small (Table 8.2), from 3.2 to 12.5 mm (± 1.3 SD) in length and from 1.6 to 6.2 mm (± 0.8 SD) in width (for *Bischofia javanica* and *Olea paniculata*, respectively).

Table 8.2 *Description of collected seeds (NI for not identified and N for the number of collected seeds). Seed's length and width in average (± one SE).*

Species name	Status [a]	N	Fruit type	Length (mm)		Width (mm)	
Citrus sp.	I	1	berry	10.9	-	5.2	-
Bischofia javanica Blume	A	1	berry	3.2	-	1.6	-
Cupaniopsis sp.	A	1	capsule (aril)	10.8	-	5.3	-
Guioa villosa Radlk	E	11	capsule (aril)	5.9	(± 0.6)	3.9	(± 0.4)
Lantana camara L.	I	45	berry	4.6	(± 0.8)	2.8	(± 0.4)
Olea paniculata R.Br.	A	11	drupe	12.5	(± 1.3)	6.2	(± 0.8)
Psidium guajava L.	I	19	berry	3.5	(± 0.5)	2.9	(± 0.5)
NI 1	-	6	-	3.9	(± 0.3)	3.5	(± 0.2)
NI 2	-	1	-	5.3	-	5.2	-
NI 3	-	2	-	7.9	(± 1.3)	4.2	(± 0.3)
NI 4	-	2	-	4.6	(± 0.7)	3.9	(± 0.4)
All		100		6.6	(± 3.3)	4.1	(± 1.4)

[a] *E for endemic species, A for autochthonous species, I for introduced species*

The quantity of seeds collected in the traps was highly temporally variable. Indeed, *ca* 60 % (80 %) of the collected seeds came from the four (eight) samples with more than 10 (5) seeds in the trap (*e.g.* we collected together 8, 13 and 16 seeds of *Olea paniculata*, *Lantana camara*, *Psidium guajava*, respectively in three different traps). Most of the seeds were collected between February and May and between August and October (Figure 8.2).

Despite the low amount of seed collected and high variability among sites, we observed a perch-effect (Figure 8.3) with higher seed arrival under *Geissois racemosa* trees (up to 10 times) than in open savannas (ranked data ANOVA $P < 0.05$, TuckeyHSD test $P > 0.05$). Compared to *Geissois racemosa* and *Pittosporum simsonii* (9.6 ± 8.5 seeds.m^{-2}.yr^{-1} and 7.0 ± 7.9 seeds.m^{-2}.yr^{-1}, respectively), the savanna species

Melaleuca quinquenervia received no significant (Tuckey HSD test, $P < 0.05$) but slightly less seeds (3.6 ± 1.1 seeds.m^{-2}.yr^{-1}).

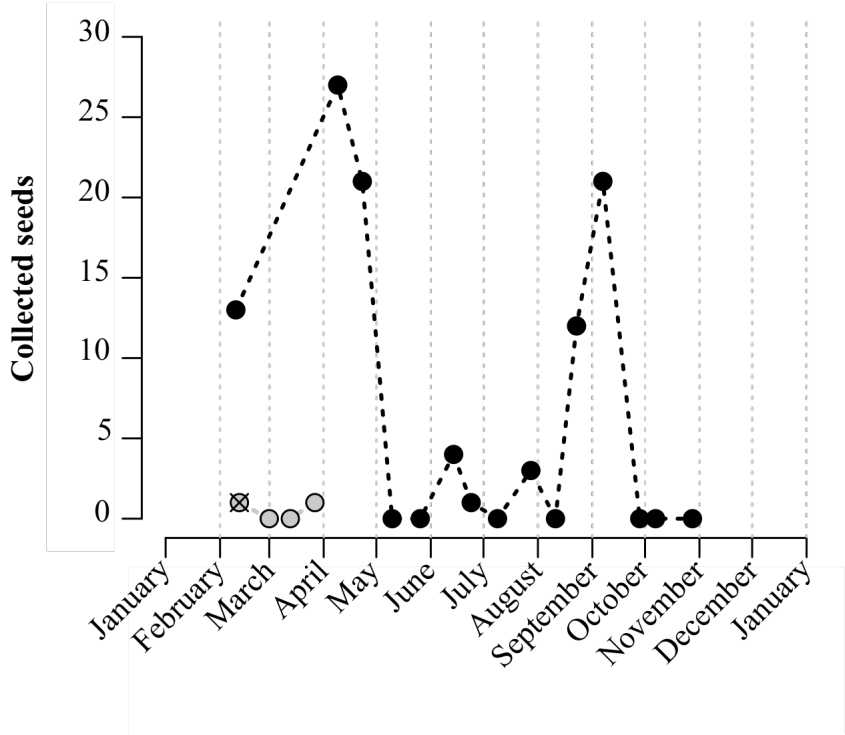

Figure 8.2 *Collected seeds along the time with black and grey circles for 2010 and 2011, respectively (the crossed-circle indicates that most of the seed-traps did not work between December 2010 and February 2011).*

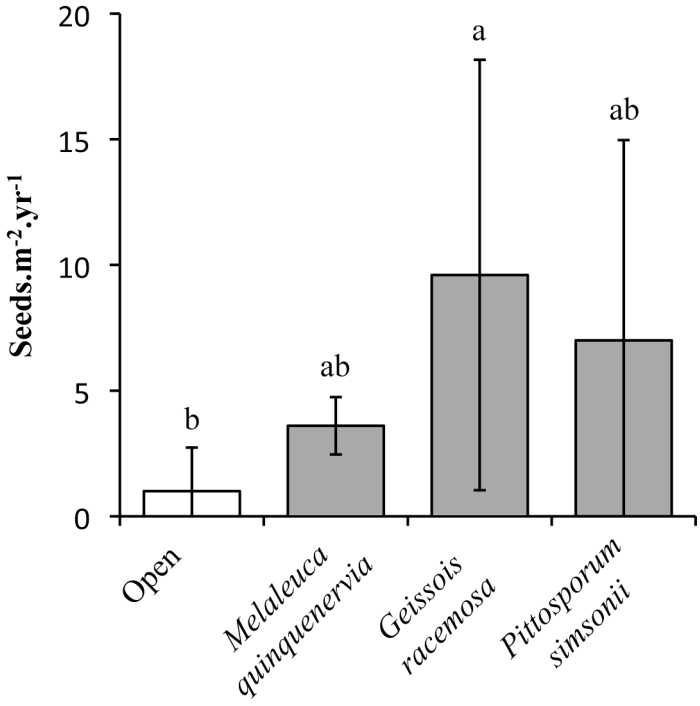

Figure 8.3 *Averaged collected seeds (± one SE) under the different treatments (different letters show significant difference in the amount of collected seed, P < 0.05, Tukey HSD test).*

8.6 Discussion

8.6.1 Low seed-rain but enhanced by perch effect

The observed higher seed arrival under trees than in open area confirms the perch-effect. In tropical regions, this process has been widely observed in abandoned pastures (Holl 1998; Slocum and Horvitz 2000), or in disturbed forest (Elmqvist et al. 2002; Shiels and Walker 2003). Our results suggest that seeds arrival is particularly higher under *Geissois racemosa*, which is one of the two studied pioneer species. Given that none of the studied species produce fleshy fruits that may attract disperser (see Slocum and Horvitz 2000), we suggest that in these wooded savannas widely dominated by *Melaleuca quinquenervia*, the denser cover offered by *Geissois racemosa* (and to a less

extent by *Pittosporum simsonii*) may explain this higher seed arrivals (but see Slocum and Horvitz 2000).

The number of bird-dispersed seeds collected (1 ± 1.3 seeds.m^{-2}.yr^{-1} in open savanna and from 3.6 ± 1.1 to 9.6 ± 8.5 under trees) was very low comparing to the other studies. For example, the number of seeds collected by Holl (1998) and Shiels and Walker (2003) under perches was more than 15 and 5-fold higher, respectively. The distance from the forest edge may explain the low seed arrival in open savanna. Indeed the seed arrival (and particularly bird-dispersed seeds) decreases rapidly in open areas with the distance from the forest edge, and seed arrival becomes almost null at 5-10 m away from the edge (*e.g.* Cubina and Aide 2001; Holl 1999; McClanahan and Wolfe 1987). The low seed arrivals under trees may also be explained by the low-forested area and the high fragmentation of the forest in the surroundings of the seed-traps (Herrera and Garcia 2010).

As in many seed-rain studies in open areas (Gonzales *et al.* 2009; Holl 1998; 1999; Zimmerman *et al.* 2000), few seeds coming from forest-species were collected in the traps. In this study the majority of the collected seeds were from invasive species (*Lantana camara* and *Psidium gujava*) or early secondary species (*Guioa villosa*) that grow into savanna. Nevertheless, the presence of several seeds coming from *Olea paniculata*, a forest species only inventoried in the larger of the two forest-fragments confirms the dispersal of seed by birds from forest to savannas. This result is likely linked to the behaviour of frugivorous birds that seldom go in open areas after feeding in forest fragments (Pizo 2004). The seeds collected in the traps were relatively small suggesting that large disperser do not dispersed seeds into savannas (see Carpenter et al. 2003 and Gailhbaud, unpublished data).

8.6.2 Implications for forest restoration

The low arrivals of seeds from secondary forest or forest trees in savannas surrounding by highly fragmented forest highlight the need of increasing artificially seed-rain or adding seedlings to restore forest. Our results suggest that planting early secondary species such as *Geissois racemosa* may increase bird-dispersed seed rain. However, studies on potentially more attractive trees such as trees that produce fleshy fruits like

Ficus spp (Guevara et al. 2004; Slocum 2001) are needed to optimise forest restoration. Planting tree islands with different tree species to attract the more diverse dispersers may also be a good way to promote forest recovery (*e.g.* Cole et al. 2010; Fink et al. 2009). However seed arrivals is only one of the barriers to forest re-colonisation (Holl et al. 2000). In the studied area, as in many places in the tropics competition with weeds and survival to fire are critical barriers that have to be overcome by management (see Lamb et al. 2005; Morrison and Lindell 2011).

8.7 Acknowledgements

We thank the ANR BDIV-07-008 project INC, the WWF-Nouvelle-Calédonie and the CNRS for funding this research and the PhD scholarship of T. Ibanez. We are grateful to Denis Maeandu-Poveu, Isabelle Gorodé et Julien Gorodé for their useful help on the field.

8.8 Appendix

Inventoried taxa in the forest fragments

Family	Species name	Status[a]	N_i	Seed dispersal	
				Birds	Other
Annonaceae	*Polyalthia nitidissima* (Dunal) Benth.	A	5	X	
Apocynaceae	*Alstonia costata* (G.Forster) R.Br.	E	1		X
Araliaceae	*Plerandra gabriellae* (Baill.) Lowry, G.M. Plunkett & Frodin, ined.	E	3	X	
Bischofiaceae	*Bischofia javanica* Blume	A	3	X	
Cunoniaceae	*Geissois racemosa* Labill.	EE	1		X
Ebenaceae	*Diospyros fasciculosa* (F.Muell.) F.Muell.	A	13	X	
Euphorbiaceae	*Codiaeum peltatum* (Labill.) P.S.Green	A	23	X	
	Omalanthus nutans (G.Forster) Guillemin	E	7	X	

Gentianaceae	*Fagraea berteroana* A.Gray.	A	1	X	
Meliaceae	*Dysoxylum roseum* C.DC.	E	4	X	
	Dysoxylum spp.	-	1	X	
Mimosaceae	*Archidendropsis granulosa* (Labill.) I.C.Nielsen	E	14		?
	Archidendropsis spp.	E	1		?
Moraceae	*Ficus fraseri* Miq	A	2	X	
	Ficus habrophylla Bennett ex Seemann	A	6	X	
	Ficus spp.	-	1	X	
Oleaceae	*Olea paniculata* R.Br.	A	5	X	
Palmae	*Chambeyronia macrocarpa* (Brongn.) Vieill. Ex Becc.	E	1	X	
Pittosporaceae	*Pittosporum simsonii* Montrouz.	E	7	X	
Phyllanthaceae	*Glochidion caledonicum* Muell.Arg.	E	1	X	

	Glochidion spp.	E	9	X	
Proteaceae	*Kermadecia sinuata* Brongn. & Gris	EE	1	X	
Rutaceae	*Acronychia laevis* Forster & G.Forster	A	10	X	
	Micromelum minutum (Forster & G.Forster) Whigt & Arn.		1	X	
Sapindaceae	*Cupaniopsis* spp.	-	4	X	
	Elattostachys apetala (Labill.) Radlk.	A	18	X	
	Guioa villosa Radlk.	E	7	X	
	NI	-	1		?
NI	NI	-	8		?

[a] EE for endemic genus, E for endemic species, A for autochthonous species, I for introduced species

9 Impacts of invasive weeds on tree regeneration: Preliminary results on the case of *Lantana camara* L.

This section presents preliminary results as supplementary material, which will not be submitted for publication.

9.1 Introduction

Competition with grass (for water, nutrients or light) is one of the main factors limiting trees establishment in savanna (Bond 2008; Sankaran et al. 2004; Scholes and Archer 1997) and competition with invasive weeds is one of the main factors limiting forest recovery in degraded areas (Holl et al. 2000; Hooper et al. 2005; Zimmerman et al. 2000). Native grasses also limit tree establishment and forest recovery (*e.g.* Davis et al. 1999; Williams et al. 2005) nevertheless invasive weeds may modify the grass cover characteristics (*e.g.* height, cover, density) and enhance the impact of grass cover on tree regeneration. For instance, Hoffmann and Haridasan (2008) showed that tree seedling survival decreases with the grass biomass, which increased with the invasion by weeds (*Melinis minutiflora* Beauv.). More recently, Ortega-Pieck *et al.* (2011) showed that tree seedling survival is lower when the grass layer is dominated by an invasive species (*Cynodon plectostachyus* (K. Schum.) Pilg.), which is twice as tall than the native ones.

Tropical islands are particularly vulnerable to weed invasions (Denslow 2003; Sherley 2000). In New Caledonia, the introduction of weeds has sharply increased since 1950 (Gargominy *et al.* 1996). According to Hequet *et al.* (2009), more than 2,000 plant species, among which 200 can be considered as invasive (*e.g. Leucaena leucocephala*, *Lantana camara*, *Melinis minutiflora* ou *Pinus caribaea* var. *hondurensis*) or potentially invasive, have already been introduced in New Caledonia. Among these species, *Lantana camara* (*Verbenaceae*) is one of the most problematic weeds at both New Caledonian (Hequet *et al.* 2009) and global scale (e.g. Dobhal *et al.* 2011; Duggin and Gentle 1998; Raghubanshi and Tripathi 2009; Ratnam *et al.* 2011).

Here we explore the hypothesis that *L. camara* slows down or stops the establishment and the growth of trees in invaded *Melaleuca quiquenervia* savanna.

9.2 Materials and methods

We selected two sites (A and B, 100 and 250 m^2, respectively) located nearby two tree islands surrounded by savannas and removed all invasive (mainly *L. camara*, Figure

9.1.A) by slashing to inventory all seedlings higher than 20 cm (Figure 9.1.B). In both sites, the *L. camara* layer was about 2 m in height.

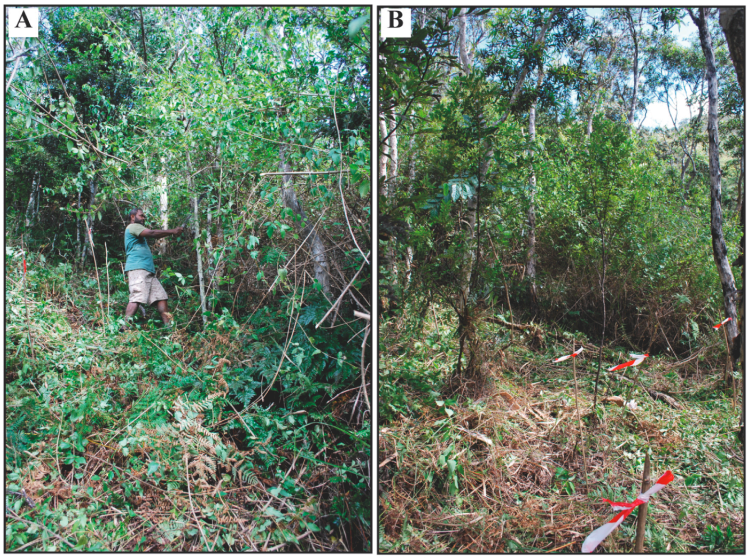

Figure 9.1 *Photographs of studied site B. (A) Cleaning of the site invaded by Lantana camara (the left side was already cleared, not the right one), note that the Lantana camara layer is widely higher than the field assistant (D. Meandu-Poveu). (B) Site after cleaning with apparent seedlings (note the height and the density of the Lantana camara layer in the background).*

9.3 Results and discussion

Seedling density was 0.42 seedling.m^{-2} in both sites (Table 9.1). Most of the inventoried seedlings were from small-tree species dispersed by birds (*Acronychia laevis*, *Glochidion caledonicum* and *Guioa villosa*) and only one seedling of wind-dispersed species (from *Geissois racemosa*) was inventoried.

Despite the lack of control sites our preliminary results suggest that *L. camara* prevents tree regeneration likely not only by affecting seedlings establishment, but also by affecting seedling survival and growth. Indeed, most of the inventoried seedlings were etiolated due to the low light availability under dense *L. camara* cover (Figure 9.1). This low light availability also limits the establishment of shade intolerant species such as *Geissois racemosa* (Ibanez *et al.* submitted-c). Moreover the dense *L. camara* cover is likely a mechanical barrier to seedlings growth.

Table 9.1 *Number of inventoried seedlings (NI for not identified, Orn. for ornithochorous and Ane. for anemochorous dispersal type).*

Species	Site A (100 m^2)	Site B (250 m^2)	Orn.	Ane.
Acronychia laevis Forster & G.Forster	16	1	X	
Elattostachys apetala (Labil.) Radlk.	0	1	X	
Geissois racemosa Labill.	1	0		X
Glochidion caledonicum Mueli. Arg.	1	26	X	
Guioa villosa Radlk.	20	69	X	
Pittosporum simsonii Montrouz.	4	7	X	
Tabernaemontana cerifera Pancher & Sebert	1	0	X	
NI	1	0		
Total	42	104		

Weeds limit tree regeneration by affecting their growth and survival (*e.g.* Hoffmann and Haridasan 2008; Ortega-Pieck *et al.* 2011), however one of the other important impacts of weeds on forest regeneration is the modification of fire regime. Indeed the fuel characteristics of invaded grass layer may conduce to more intense fire (*e.g.* Hoffmann et al. 2004; Mistry and Berardi 2005), likely leading to higher tree mortality (see Michaletz and Johnson 2007). Moreover, weeds may also indirectly increase fire frequency as Humans light fires to clear area invaded by weeds such *L. camara*, which obstruct their way.

Several methods exist to manage weeds (e.g. Denslow 2007; Love *et al.* 2009), including mechanical (clipping), physical (burning), chemical (herbicide) and biological (competitor, predator, pathogen) controls. However, to optimise weeds managements and avoid further environmental degradation, a good knowledge of both weeds ecology and the impacts of control methods on ecosystems are needed. For instance, burning *L. camara* is likely counterproductive as *L. camara* can resprout after fire (Love *et al.* 2009), while fire open areas and may degrade forest edge, which in turn support the expansion of *L. camara* populations (Duggin and Gentle 1998; Love *et al.* 2009).

Chapitre III

Résumé du chapitre

Dans le troisième chapitre de cette thèse, nous nous intéressons aux zones de transition entre savanes et forêts denses humides qui constituent des zones charnières dans la dynamique des paysages étudiés.

Dans la première section de ce chapitre (section 10), ces zones de transitions sont analysées en termes de structure et de composition de la végétation afin de mieux comprendre leurs dynamiques. Des changements abruptes ou graduelles de la végétations suggèrent une alternance de phases instables (expansion ou contraction forestière) et stables (maintient de la lisière forestière). Notre hypothèse de travail étant que le régime d'incendie et le principal facteur dirigeant cette dynamique, des variations dans la végétation, les ignitions ou le climat pourraient diriger ces alternances de phases. Les variations microclimatiques au niveau de la lisière forestière soumise aux effets de bords pourraient notamment rendre celle-ci plus ou moins vulnérable aux incendies au cours du temps.

Dans la deuxième section de ce chapitre (section 11), nous analysons donc la variabilité microclimatique le long de ces même transects. Nous testons l'hypothèse selon laquelle des effets de bords microclimatiques rendent la lisière forestière vulnérable aux incendies se propageant en savane durant la saison sèche. Contrairement à nos attentes, la transition des conditions microclimatiques entre la savane et la forêt a été très abrupte tout au long de la période étudiée et a été situé à l'extérieur de la forêt. Nous suggérons que ces résultats sont liés au fait que l'année étudiée était anormalement humide (épisode *La Niña*), et que dans de telles conditions la vulnérabilité de la lisière forestière aux feux de savane est relativement faible, alors que les conditions plus humides le long de la lisière forestière an savane pourraient favoriser l'expansion de la forêt. Enfin, durant les périodes anormalement sèches (*El Niño*), la zone de transition des conditions microclimatiques entre la savane et la forêt devrait se décaler vers l'intérieur de la forêt, ce qui dessécherait le sous-bois et rendrait la lisière forestière plus vulnérable aux feux de savanes.

10 Key species and ecological structure detecting savanna-forest transition zone dynamics in New Caledonia

This section is in preparation for submition to *Journal of Tropical Ecology* as the following research paper :

Ibanez, T., Munzinger, J., Gaucherel, C., Curt, T. and Hély, C., (in prep.). Key species and ecological structure detecting savanna-forest transition zone dynamics in New Caledonia, in preparation for submition to *Journal of Tropical Ecology*.

Notice: Some data are missing but will be completed soon (diameter at breast height of the individuals located in the transect 2 between -20 and 15 m, thus we temporarily set these diameter to 5 cm).

10.1 Résumé

La déforestation est une des principales causes de perte de biodiversité dans les tropiques. Une conséquence directe de la déforestation et de la fragmentation des forêts est l'augmentation de l'importance des zones de transition entre les fragments forestiers et de leur matrice environnante tels que la savane. Ces zones de transition sont des entités dynamiques, complexes, multivariées et multidimensionnelles. Dans cette étude, nous proposons d'étudier la structure et la composition de la végétation le long de trois transects allant de la savane à l'intérieur de la forêt afin de mieux comprendre la dynamique spatio-temporelle de ces zones de transition. Nous faisons l'hypothèse que la structure de la zone de transition entre savane et forêt avec des changement abruptes (frontières) et / ou des changements plus progressifs (écotones) dans les assemblages floristiques et la structure des population peut mettre en avant leur dynamique spatio-temporelle. La présence d'un écotone allant de la lisière à l'intérieur de la forêt, caractérisée par des changements graduels dans la composition des espèces et la structure des populations associées à la présence d'arbres 'reliques' de savanes, a mis en avant que la lisière de la forêt s'est probablement déplacé d'environ 40 m vers la savane au cours des dernières décennies par succession secondaire. En revanche, la présence d'une frontière entre la savane et le début de cet écotone, caractérisée par des changements abrupts, souligne que cette expansion forestière a probablement été stoppée. Ceci suggère que différentes phases peuvent alterner dans la dynamique de la zone la transition entre la savane et la forêt; des phases 'stable' où la zone de transition ne bouge pas, et des phases 'instable' où la zone de transition se déplace ou se dilate vers la savane (expansion de la forêt) ou la forêt (forêt contraction). Les passages de phases 'stable' à 'instable' et vise et versa sont probablement dues à des changements dans le régime de perturbation. Enfin, notre étude souligne la nécessité des analyses multivariées pour comprendre la dynamique de ces zones complexes de transition entre savane et forêt.

Mots-clés : composition floristique**,** écotones**,** fenêtres glissantes, feux, frontières.

10.2 Abstract

Deforestation is one of the main causes of biodiversity loss in the tropics. A direct consequence of deforestation and forest fragmentation is the increase of the importance of the transition zones between forest fragments and their surrounding matrix such as savanna. These transition zones are dynamic, complex, multivariate and multidimensional entities. We studied the structure and the composition of the vegetation along three transects from savanna to forest interior to better understand the spatio-temporal dynamics of the transition zones. We make the hypothesis that the structure of the transition zone between savanna and forest with sharp (boundaries) and / or gradual transitions (ecotones) in floristic assemblages and population structures may point out its spatio-temporal dynamics. The presence of an ecotone from the forest edge to the forest interiors characterised by gradual changes in species composition and population structures associated with the presence of remnant savanna trees, pointed out that the forest edge has likely shifted *ca* 40 m toward savanna during the last decades by secondary succession. However, the presence of a boundary between the savanna and the beginning of this ecotone characterised by sharp change, points out that this forest expansion has likely been stopped. This suggest that different phases may alternate in the savanna-forest transition zone dynamics; 'stable' phases where the transition zone does not move, and 'instable' phases where the transition zone moves or expands toward savanna (forest expansion) or forest (forest contraction). Changes over 'stable' and 'instable' phases are likely due to changes in disturbance regime. Finally, our study highlights the need of multivariate analyses to understand such complex savanna-forest transition zone dynamics.

Keywords : boundary, fire, floristic composition, ecotone, moving window analysis.

10.3 Introduction

Deforestation is one of the main causes of biodiversity loss in the tropics (Brooks *et al.* 2002; Wright and Muller-Landau 2006a) and is still alarming high (FAO 2010). A direct consequence of deforestation and forest fragmentation is the increase of the importance of the transition zones (Fagan *et al.* 2003) between forest fragments and their surrounding matrix such as savanna (see Prevedello and Vieira 2010). Here, we propose to study the structure and the composition of savanna-forest transition zones to better understand their spatio-temporal dynamics, which is critical for landscape management and biodiversity conservation (Cadenasso *et al.* 2003).

Forest-matrix transition zones also called interfaces, boundaries, ecotones, borders or edges are highly dynamic (Cadenasso *et al.* 2003; Fagan *et al.* 2003; Hufkens *et al.* 2009; Strayer *et al.* 2003) and affect the functioning of both the forest and the matrix through the so-called 'edge effects' (Fonsca and Joner 2007; Murcia 1995). Ecological transition zones are complex, multivariate and multidimensional entities (Hufkens *et al.* 2009), which can be mainly characterised by their (i) origin and maintenance, (ii) spatial structure, (iii) function, and (iv) temporal dynamics (Strayer *et al.* 2003). In this study, we explored how the spatial structure and the composition of a transition zone may reflect its temporal dynamics.

In the tropics, forest is often surrounded by savanna, which may be an alternative stable state of forest (Scheffer and Carpenter 2003; Warman and Moles 2009). Forest and savanna are two very contrasting ecosystems in terms of structure, composition and functioning, making the analysis of their transition zones and its dynamics particularly interesting. Savanna-forest transition zones may either be very sharp or gradual with successional transition reflecting forest expansion or contraction. At global scale, the savanna-forest distribution is mainly driven by climatic condition and particularly by the amount of rainfall (Bond 2008; Staver *et al.* 2011a), while at regional and local scales disturbances such as fire and grazing are through their regime the mains drivers (*e.g.* Gardner 2006; Lehmann *et al.* 2008; Midgley *et al.* 2010). Hence, the dynamics of savanna-forest transition zone – forest expansion or contraction – are likely closely linked to disturbance regime.

In the New Caledonian biodiversity hotspot (Mittermeier *et al.* 2004; Myers 1988), on volcano-sedimentary substrates, rainforest, mainly replaced by savanna, have dramatically contracted since the Melanesian settlements (-3500 years BP) and mainly since the European one (at the end of the 18th century) due to increases in anthropogenic disturbances (Jaffré *et al.* 1998). As results, forest are fragmented at low and middle elevation (e.g. Ibanez *et al.* submitted-b) and have taken refuge in inaccessible area (Jaffré *et al.* 1998). Today anthropogenic fires, which mainly spread into savannas (Curt *et al.* in prep.) but can penetrate in the savanna-forest transition zones, erode forest (Hély *et al.* in prep.) and are likely its main threats (Pascal *et al.* 2008). However, the structure and the composition of such savanna-forest transition zones and the processes involved in their spatio-temporal dynamics, are poorly known in New Caledonia.

Owing to the lack of consensus regarding the terms used by ecologists to describe ecological transition zones (Cadenasso *et al.* 2003; Hufkens *et al.* 2009; Strayer *et al.* 2003), it is necessary to clearly define the terms used to make studies comparable. The terms boundary and ecotone, both referring to the zone that separate two different ecosystems (*e.g.* savanna and forest) are widely used as synonyms. We suggest calling ecotones, special boundaries in which the studied statistics highlight a gradual transition, while all others transition (more or less sharp) are called boundaries. Hence, we suggest that according to the studied statistics, either a boundary or an ecotone or both, may constitute a transition zone between forest and savanna. We also used the terms forest core and savanna core in opposition to the forest and savanna within the savanna-forest transition zone. Finally, forest edge refers to the savanna-forest borderline visually defined on the field.

In this study we performed multivariate analyses on the structure and the composition of the savanna-forest transition zone in order to better understand its spatio-temporal dynamics. We make the hypothesis that the structure of the savanna-forest transition zone with sharp (boundaries) and / or gradual transitions (ecotones) in floristic assemblages and population structures may point out its spatio-temporal dynamics.

10.4 Materials and methods

10.4.1 Data collection

Three replicate transects (T1 to T3, 120 m in length and 20 m in width), from savanna to forest interiors were positioned perpendicularly to the forest edge (Figure 10.1). The forest edge was visually determined for each transect in the field according to clear discontinuities simultaneously in tree density, composition and grass cover. All distances measured along each transect and used in the analysis referred to this forest edge (*i.e.* transects started at -30 m in the savanna core and finished at 90 m in the forest core).

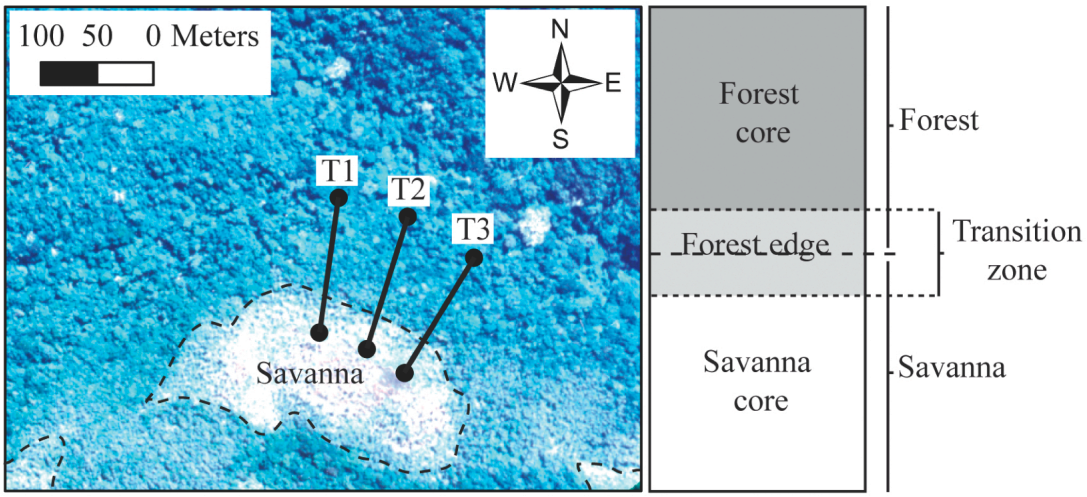

Figure 10.1 *Aerial photograph (from 1997) with the position of the three studied transects.*

On each transects, all trees with a diameter at breast height (DBH) ≥ 5 cm and located within the 10-m buffer on both sides of the transects were mapped, with a 10-cm uncertainty for their location as we used an ultrasonic hypsometer (Vertex IV) and tapes. Trees were labelled with permanent forestry tags and directly identified on the field or sampled to be identified at the herbarium of the centre IRD of Nouméa (NOU) using the *Flore de Nouvelle-Calédonie et Dépendances* (Aubréville *et al.* 1967-present) and identified material. Identified samples have been deposited at NOU and fertile

samples were kept as voucher. Plant names are following Florical (Morat *et al.* in prep.), while morphospecies names were given to unidentified samples. Data were integrated in NC-PIPPN database (New Caledonia Plant Inventory and Permanent Plot Network).

10.4.2 Transect structure and composition analyses

We combined different types of analyses described bellow in order to identify boundaries and ecotones and finally characterise the savanna-forest transition zone. In order to have a general view of the transition patterns, we computed the profiles of each studied statistics (reflecting vegetation structure and composition) along the three transects using moving windows. Then, to identify discontinuities in these profiles, we applied split moving window dissimilarity analysis (SMWDA, see Cornelius and Reynolds 1991; Ludwig and Cornelius 1987), the higher discontinuities were considered as boundaries. As suggested by Hennenberg *et al.* (2005a), SMWDA were associated to moving window regression analysis (MWRA, see Walker *et al.* 2003) to identify the position and the width of the identified discontinuities. For the species composition analysis, SMWDA and MWRA were completed by detrended correspondence analysis (DCA) to identify different floristic assemblage and different floristic zones along the transects (Choesin and Boerner 2002; Hufkens *et al.* 2009).

In SMWDA, a window is moved along the transect according to a defined step (1 m in this study) and a dissimilarity value is calculated for each window-midpoint position as the Euclidean distance for a vegetation statistics between the two halves on the window. Dissimilarity values were standardized relatively to the overall expected mean dissimilarity and standard deviation (Z-score) and plotted against the window-midpoint positions along the transect. As suggested by Cornelius & Reynolds (1991), a dissimilarity profile was computed for each transect as the mean of dissimilarity profiles (mean Z-score) computed for four different window sizes (in this study 40, 30, 20 and 10 m) in order to reduce SMWDA scale-dependency. Boundaries between savanna and forest were identified by the greatest mean Z-scores peak located above the 95 % confidence interval ($Z = 1.65$) of the null distribution. Others peaks were interpreted as

secondary discontinuities such as these found in the forest, while areas of lower mean Z-scores indicate gradual shifts in vegetation (Boughton *et al.* 2006; Cornelius and Reynolds 1991).

We used MWRA to measure the width of the discontinuities identified by SMWDA. For each window-midpoint position, we computed the slope of the linear least square regression between the five consecutive mean Z-scores (the midpoint and two points on each sides) and position along the transect. The two borders defining the width of a boundary or a discontinuity is determined by the maximum positive slope value and the minimum negative one (see Hennenberg *et al.* 2005a for more details).

Boundaries and secondary discontinuities in vegetation structure were assessed by analysing stem density and relative frequencies of three DBH classes based on the median (10 cm) and the third quartile (20 cm) DBH distribution. Concerning the vegetation composition, we analysed the species richness, the Shannon diversity index and the relative frequencies of each species. As most of the species were poorly represented along each transect, we only analysed the relative frequencies of species represented by more than five individuals. For each transects, we computed dissimilarities in species composition as the mean of dissimilarities in the relative frequencies computed fore each species.

To complete the analysis of discontinuities in vegetation composition, we performed DCA on each transect using the R package *vegan*. Each transect was devised in 12 plots (10 x 20 m) and DCAs were performed on the relative species frequencies. As for dissimilarity analysis, we only worked with species represented by five or more individuals on the transect. We grouped plots and species according to their positions on the first axis of the DCAs using hierarchical ascendant classification and the Ward grouping method to identify different floristic groups and assemblages. All statistical analyses were performed using the R 2.9.2 environment for statistical computing (R Development Core Team 2009).

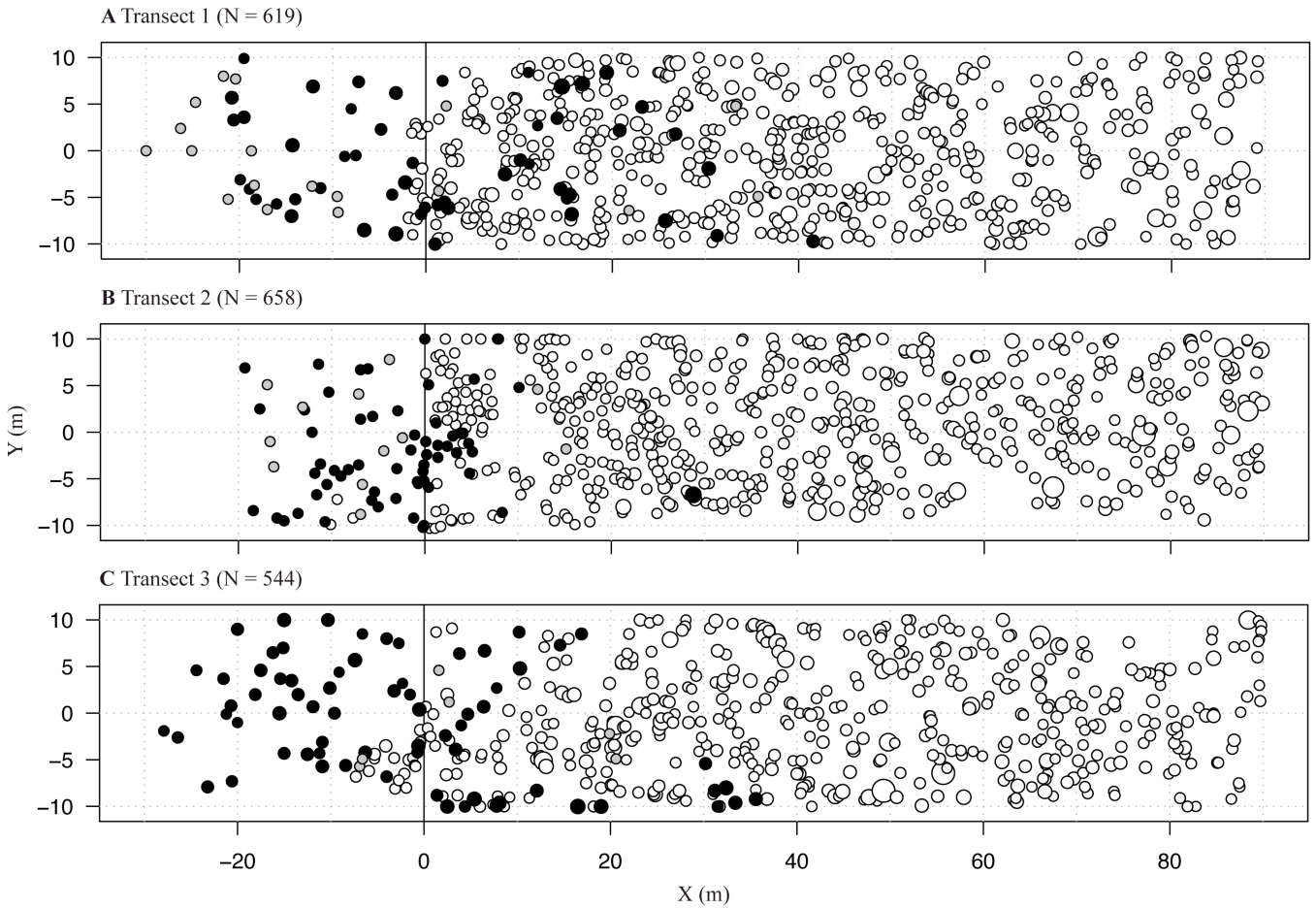

Figure 10.2 *Maps of the three studied transects. Black and grey circles represent Melaleuca quinquenervia alive and dead trees, respectively and white ones represent other trees species. The diameters of the circles are proportional the DBH of the trees. The black vertical line represents the forest edge as determined on the field.*

10.5 Results

Along the three studied transects, a total of 1783 alive trees belonging to 44 families and 134 *taxa* were inventoried (Appendix I). More than 92 % and 6 % of them were identified at the species and genus levels, respectively. Both, the number of stems (601, 644 and 538) and inventoried *taxa* (68, 85 and 87) were quite similar in the three transects (T1, T2 and T3, respectively).

Along each transect, *ca* 75 % of the inventoried *taxa* were represented by fewer than five individuals. Conversely, the 25 % remaining (*i.e.* 33 *taxa* among the 134 inventoried) represented about 70 % of the total inventoried trees (Appendix II). Among inventoried families, *Araliaceae* (mainly, *Plerandra* spp.), *Cunoniaceae* (mainly, *Geissois* spp. and *Weinmannia serrata*), *Meliaceae* (mainly *Dysoxylum* spp.) and *Sapindaceae* (mainly *Cupaniopsis* spp.) were particularly abundant, representing 6.4, 5.5, 14.2 and 18.2 % of the total inventoried trees, respectively (Appendix I).

10.5.1 Savanna remnant trees in forest, indicators of forest expansion

The dominant savanna tree *Melaleuca quinquenervia*, which is a shade intolerant species (Serbesoff-King 2003), was inventoried in the forest part of the transects up to 41.6, 28.8 and 35.6 m in the forest interior (in T1, T2 and T3, respectively), suggesting that forest had expanded into the neighbouring savanna (Figure 10.2). As a result, each transect could be divided in three zones, (i) the savanna core, (ii) the savanna-forest transition zone, which roughly corresponded to the zone where forest have expanded (called below recovering forest), and (iii) the forest core.

The savanna-forest transition zone was characterized by a decrease in *M. quinquenervia* tree density (Figure 10.3) with sharper decrease in small tree density than largest one (Figure 10.4). These results suggested a density dependent mortality of *M. quinquenervia* trees within the recovering forest and a gradual replacement of them by secondary forest species. This hypothesis was supported by the presence of dead *M. quinquenervia* in the recovering forest (Figure 10.2).

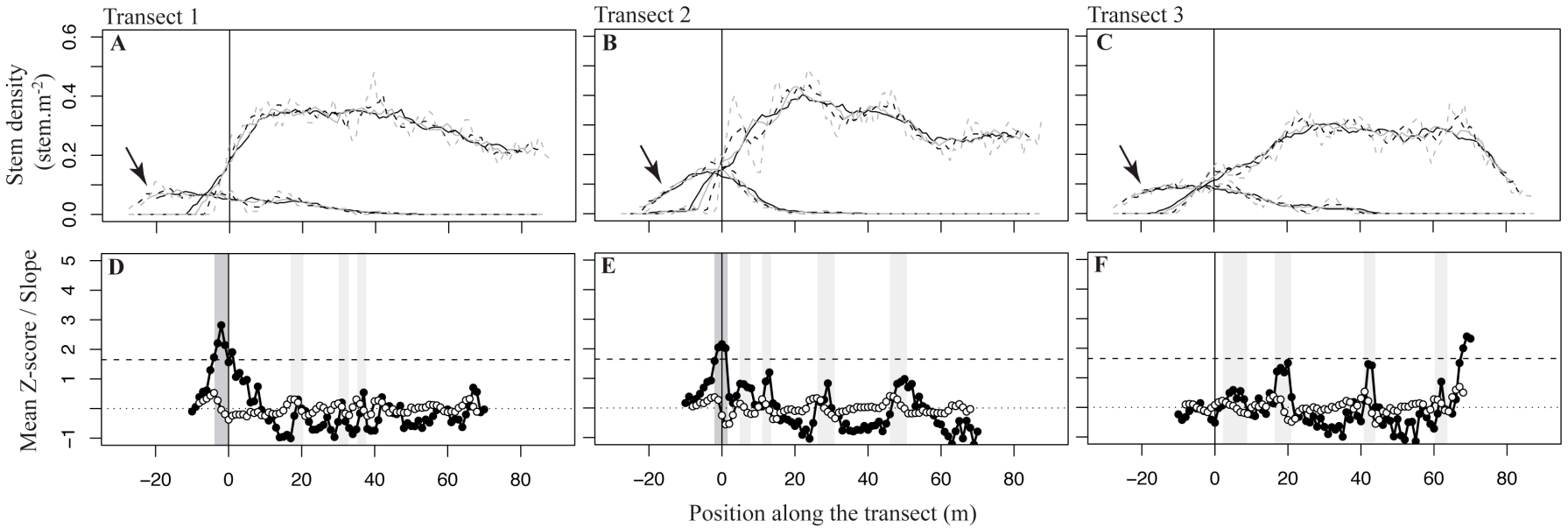

Figure 10.3 *Stem density profiles (A, B and C) of both Melaleuca quinquenervia (arrows) and all others tree species pooled together for different moving windows sizes (black, grey, black dashed and grey dashed lines for 20, 15, 10 and 5 m, respectively) and associated dissimilarity profiles (D, E and F). Dark- and light- grey areas represent the principal (boundary) and secondary discontinuities determined from mean Z-score (black points) peaks and slope from MWRA (white points). The horizontal dashed line represents the one-tailed 95 % confidence interval used as significant level of the SMWDA to detect discontinuities borders and the horizontal dotted line represents the zero-baseline of slope from MWRA.*

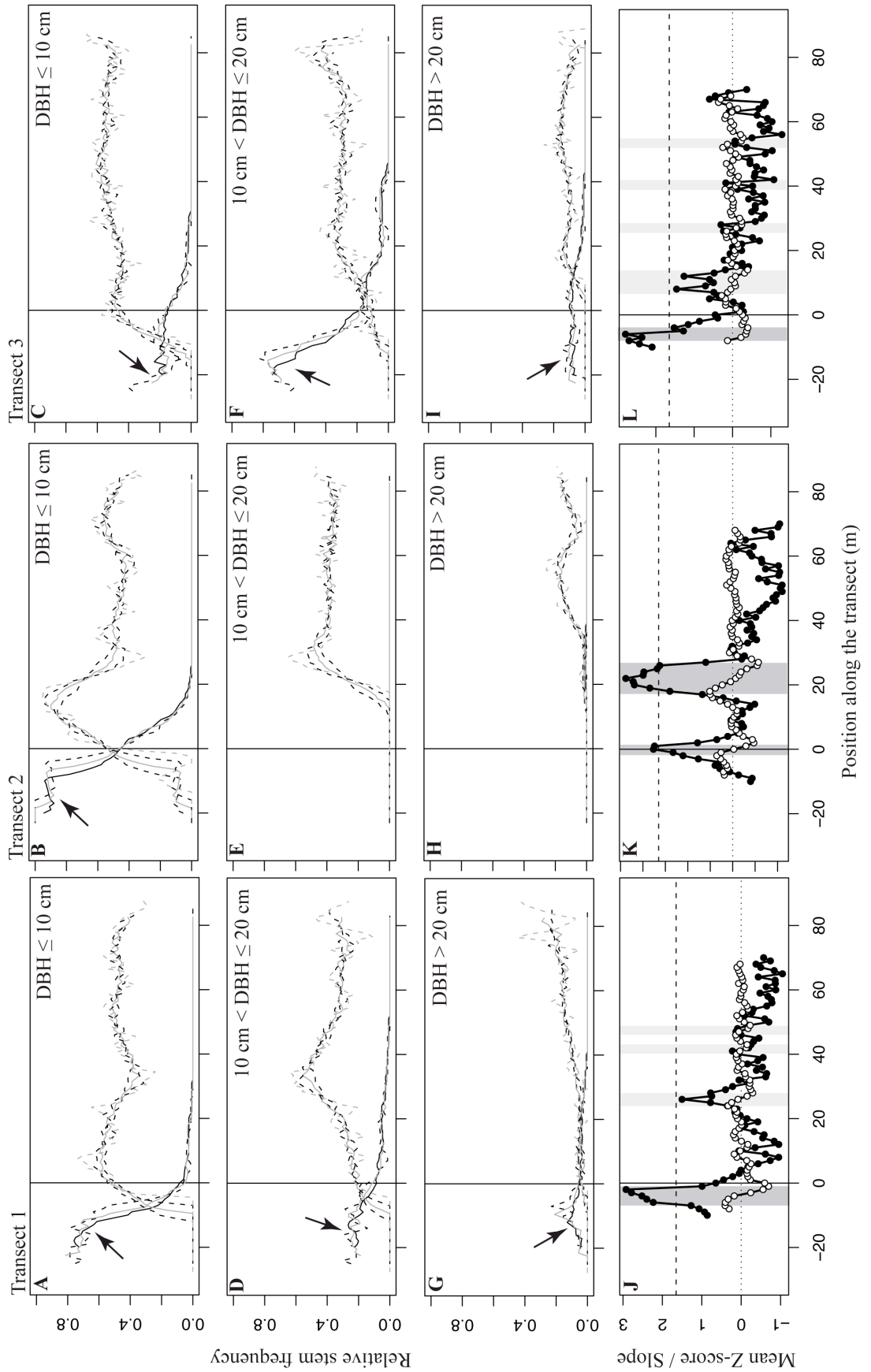
Transect 1
Transect 2
Transect 3
A
B
C
D
E
F
G
H
I
J
K
L
DBH ≤ 10 cm
10 cm < DBH ≤ 20 cm
DBH > 20 cm
Relative stem frequency
Mean Z-score / Slope
Position along the transect (m)

Figure 10.4 *(previous page) Relative stem frequency profiles of both Melaleuca quinquenervia (arrows) and all others tree species pooled together for different DBH classes (A, B and C for DBH ≤ 10 cm, D, E and F for 10 cm < DBH ≤ 20 cm and, G, H and I for DBH ≤ 20 cm) and different moving windows sizes (black, grey, black dashed and grey dashed lines for 20, 15, 10 and 5 m, respectively) and associated dissimilarity profiles (J, K and L). Key to interpreting dissimilarity profiles as in* Figure 10.3. *Notice: DBH of the individuals located in the transect 2 between -20 and 15 m are missing and were temporarily set to 5 cm.*

The inverse pattern was observed with non-*M. quinquenervia* species (hereafter referred as forest species) with a sharp increase in stem density (Figure 10.3), mainly due to an increased in small forest tree (DBH < 10 cm) density, while the increase in density of the medium trees (10 cm ≤ DBH< 20 cm) was more gradual and even more for the biggest ones (DBH ≥ 20 cm, Fig. 4). Several secondary discontinuities in forest species stem density (Figure 10.3) and frequencies of the different DBH classes (Figure 10.4) were highlighted by SMWDA and MWRA the recovering forest and the forest core. Most of these discontinuities, highlighted by 5 m and 10 m moving windows profiles, were due to small-scale discontinuities, which may reflect local disturbances such as tree fall. At larger scales (15 m and 20 m moving windows profiles) forest species stem density globally decreased gradually (Figure 10.3) while the frequency of large individuals of forest species continued to increase gradually (Figure 10.4) supporting the successional gradient hypothesis in the recovering forest.

Species richness and the Shannon diversity index also sharply increased at the beginning of savanna-forest transition zone (Figure 10.5). However, contrarily to the Shannon diversity index, which was relatively high and constant along both the recovering forest and the forest core zones, the species richness showed noticeable secondary discontinuities. Indeed, sharp increases in species richness for large scale windows (15 and 20 m) were observed around 40, 60 and 30 m in the forest interior for T1, T2 and T3, respectively. These secondary discontinuities may correspond to old savanna-forest boundaries.

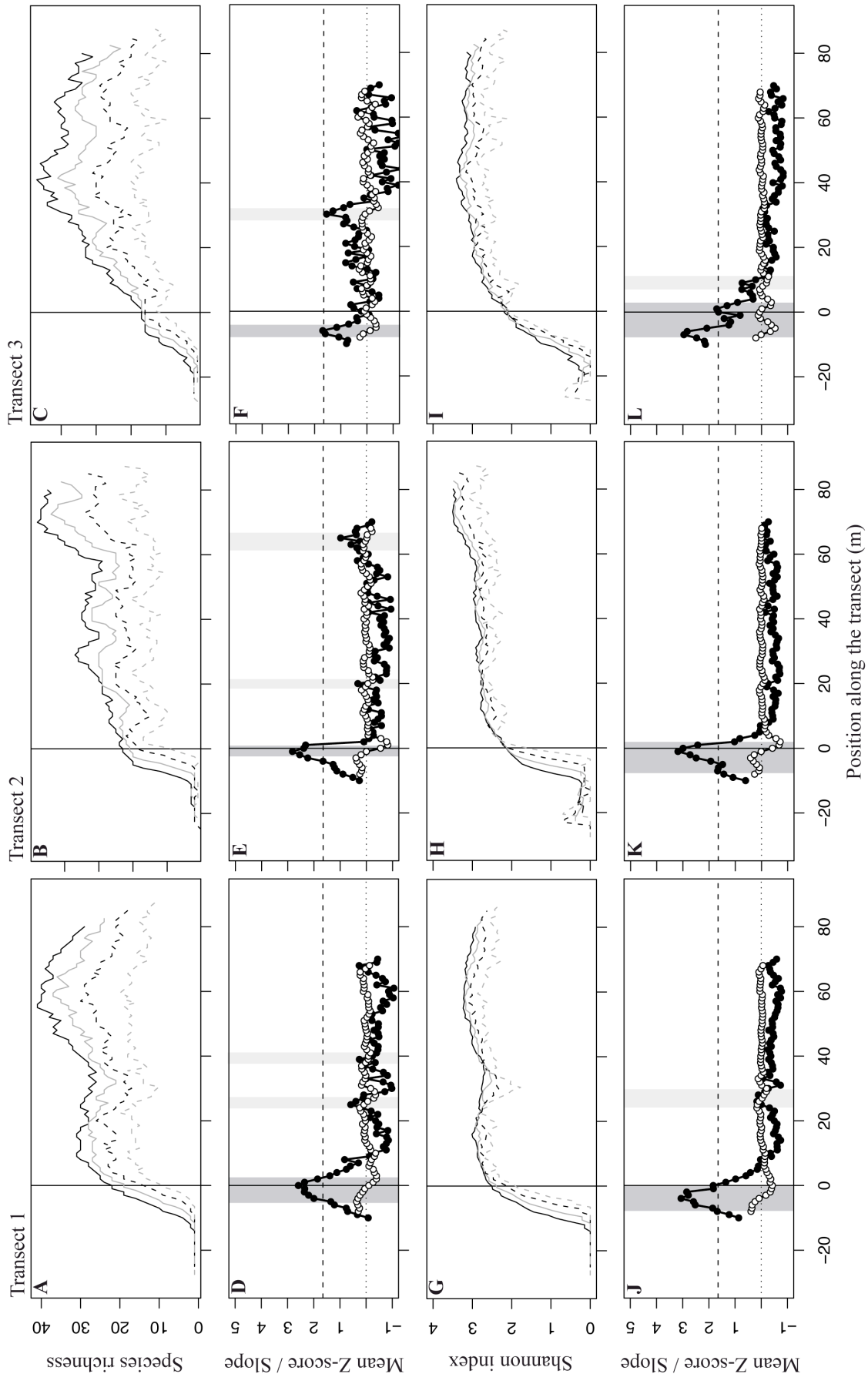
Transect 1
Transect 2
Transect 3
A
B
C
D
E
F
G
H
I
J
K
L
Species richness
Mean Z-score / Slope
Shannon index
Mean Z-score / Slope
Position along the transect (m)

Figure 10.5 (previous page) *Species richness (A, B and C) and Shannon diversity profiles (G, H and I) for different moving windows sizes (black, grey, black dashed and grey dashed lines for 20, 15, 10 and 5 m, respectively) and associated dissimilarity profiles (D, E, F and J, K, L, respectively). Key to interpreting dissimilarity profiles as in* Figure 10.3.

10.5.2 Floristic groups and forest succession patterns

The distribution of the species along the savanna-forest transects was highly structured. In terms of floristic composition, three distinct zones (although fuzzier in T3), corresponding to the savanna core, the recovering forest (which can be considered as the ecotone) and the forest core, were pointed out by both DCAs and SMWDAs (Figure 10.6). In each transect, three floristic groups were pointed out by DCAs. The first one, encompassed the savanna species (*M. quinquenervia*), and an assemblage of species, which we considered to be 'pioneer' species, and we hypothesised that the two others identified floristic groups corresponded to 'post-pioneer' and 'forest' (see Appendix I and II). The recovering forest was dominated by 'pioneer' species belonging to *Araliaceae* (mainly *Plerandra* spp. and *Meryta* spp.), *Cunoniaceae* (mainly *Geissois* spp. and *Weinmannia serrata*) and 'post pioneer' species belonging to *Phyllantaceae* (mainly *Glochidion billardierei*) and *Sapindaceae* (mainly *Cupaniopsis* spp. and *Guioa* spp.). Conversely, the forest core was dominated by 'forest' species belonging to *Clusiaceae* (mainly *Garcinia* spp.), *Ebenaceae* (*Diospyros* spp.) *Lauraceae* (*Cryptocarya* spp.), *Meliaceae* (mainly *Dysoxylum* spp.), *Monimiaceae* (*Hedycarya* spp.) and *Moraceae* (*Ficus* spp. and *Sparattosyce dioica*).

Although the species diversity was high in both the recovering forest and the forest core zones, some *taxa* were dominant. Indeed, *Cupaniopsis* spp. which encompassed seven species in the studied transects represented 20.2, 19.7 and 17.8 % of the total inventoried trees in the secondary forest ecotone zones in T1, T2 and T3, respectively. Similarly, *Dysoxylum* spp. encompassed six species in the studied transects and represented 19.2, 27.1 and 22.0 % of the total referenced trees in the forest core zones in T1, T2 and T3, respectively. However, the composition and the abundance in *Cupaniopsis* spp. and *Dysoxylum* spp. differed among transects.

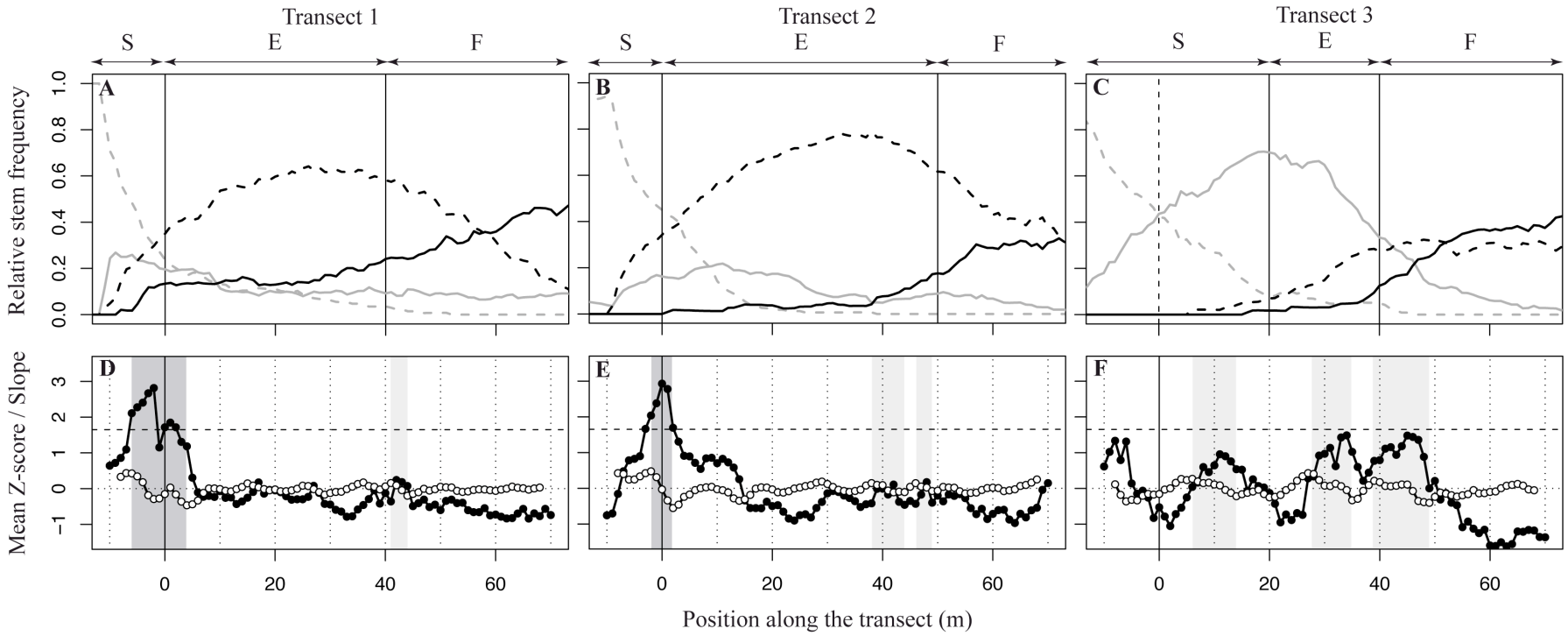

Figure 10.6 *Discontinuities in vegetation composition from SMWDA and DCA computed on species relative frequencies. Relative stem frequency (A, B and C) of groups of species pointed by DCAs: grey dashed lines for Melaleuca quinquenervia, full grey lines for the 'pioneer' group, black dashed lines for the 'post-pioneer' group and full black lines for the 'forest' group. Vertical full lines and horizontal arrows represent the three area ('S' for savanna, 'E' fore ecotone and 'F' for forest) discriminated by the DCAs. On dissimilarity profiles (D, E and F), verticals dotted lines represent the limit of the 10 m x 20 m plots defined for DCAs. Key to interpreting dissimilarity profiles as in* Figure 10.3.

For instance, *Dysoxylum rufescens* subsp. *dzumacense* dominated the forest core in T1 and T2, while it was not inventoried in T3, this last transect being dominated by *Dysoxylum macranthum*.

Profiles of relative frequency of these floristic groups illustrated, with a sharp transition between the savanna core and the recovering forest, that the process of forest expansion has been stopped (Figure 10.6). Indeed, we suggest that if this process has not been stopped, this transition would be more gradual. However, although the process of forest expansion has been stopped, gradual change between the recovering forest and the forest core suggested that the succession was still ongoing. The savanna core was mainly dominated by *M. quinquenervia*, while within a narrow boundary, the savanna also encompassed 'pioneer' and 'post-pioneer' species. The recovering forest zone (or ecotone) was dominated by 'post-pioneer' species, while the frequency of 'pioneer' and 'forest' species decreased and increased gradually, respectively. In forest core, 'forest' species frequency continued to increase while the frequency of 'post-pioneer' sharply decreased.

The compilation of the results of our multivariate analysis of the structure of the savanna-forest transition zone highlighted their complexity (Table 10.1). According to both the different studied statistics and transects, either a boundary or an ecotone or both may constitute the transition zone, and their positions were variable. Nevertheless, a global pattern could be pointed out, considering all statistics together, the transition zones consisted of both a narrow boundary characterized by sharp changes (mostly situated on the savanna side and encompassing the forest edge) and a broader ecotone characterized by gradual changes, corresponding here to the recovering forest.

Table 10.1 *Characterization of the savanna-forest transition zone. Sharp increase (↑) or decrease (↓) indicates the presence of a boundary, whereas gradual increase (↗) or decrease (↘) indicates the presence of an ecotone. Estimations of the boundaries and ecotones positions are given by their two border positions (rows 'Boundary' and Ecotone').*

Statistics	Species	DBH Classes	Transect 1	Transect 2	Transect 3
Stem density	M. quinquenervia	All	↘	↓	↘
	Others		↑ ↘	↑ ↘	↗
		Boundary	-4 m / 0 m	-2 m / 2 m	-
		Ecotone	0 m / ≥ 40 m	0 m / ≥ 30 m	0 m / ≥ 35 m
DBH classes	M. quinquenervia	DBH <= 10	↓		↘
		10 < DBH <= 20	↘		↓ ↘
		DBH > 20	↘		↘
	Others	DBH <= 10	↑ ↘		↑
		10 < DBH <= 20	↗		↗
		DBH > 20	↗		↗
		Boundary	-7 m / -1 m		? / -4 m
		Ecotone	0 m / *ca* 40 m		0 m / *ca* 40 m
Species richness	All	All	↑	↑	↗
		Boundary	-5 m / 3 m	-3 m / 1 m	
		Ecotone	-	-	-

Shannon index	All	All	↑	↑	↑
		Boundary	-8 m / 0 m	-7 m / 2 m	-7 m / 3 m
		Ecotone	-	-	-
Floristic groups	Pioneer species	All	↑ ↘	↑ ↘	↗ ↘
	Post pioneer species		↗ ↘	↗ ↘	↗
	Forest species		↗	↗	↗
		Boundary	-6 m / 4 m	-2 m / 2 m	-
		Ecotone	0 m / *ca* 40 m	0 m / *ca* 50 m	20 m / *ca* 40 m

10.6 Discussion

10.6.1 Species distribution and dominance

The gradual decrease in *M. quinquenervia*'s stem density and the gradual increase in 'forest' tree species's suggest that the forest has expanded on savanna by secondary succession pushing the forest edge *ca* 40 m toward savanna during the last decades. Indeed, as Hennenberg *et al.* (2005b) we exclude the hypothesis that the presence of some savanna remnant trees in forest results from the encroach of savanna in forest. During forest expansion, the establishment and the growth of secondary forest species likely shade *M. quinquenervia,* which is a shade intolerant species (Serbesoff-King 2003), and cause its density dependant mortality. As a result, only the largest individuals, keeping a part of their crown above the secondary forest canopy persist and point out the past presence of savanna and thus the forest expansion.

Although the forest expansion has likely been stopped by an increase in savanna fire frequency and / or intensity (which the potential causes are discuss further), three points suggest that within the recovering zone the forest succession has continued in the successional forest, (i) the relative low frequency of 'pioneer' species compare with the 'post-pioneer' ones, (ii) the gradual increase of 'forest' species density, and (iii) the relatively high species richness and diversity. The Shannon diversity index of the recovering forest and the forest-core along the studied transects (H' = about 3) were sensibly higher than the ones of early secondary forests measuring in the same landscape (H' = 0.75 ± 0.27 in average, see Ibanez *et al.* submitted-c) but were of the same order as those of the forest core (H' = 3.18 ± 0.38 in average, Munzinger pers. com.) located in the same landscape as well.

Contrarily to what Banfai and Bowman (2007) showed in their study in Australia, the floristic assemblage between the recovering forest and the forest-core sensibly differ. Indeed, although the species composition change is gradual along the transect, two different floristic assemblages were identified (see Appendix I and II). These results complete the observations of Jaffré et al. (1997b) on post-fire re-colonisation of forest in New Caledonia.

Species belonging to *Sapindaceae* and *Meliaceae* were the most represented in term of stem density. Such dominance was also observed by Jaffré and Veillon (1995) and is likely representative of rainforest on volcano sedimentary substrate in New Caledonia. We suggest that *Sapindaceae* (here mainly *Cupaniopsis* spp.) are representative of successional forest, while *Meliaceae* (here mainly *Dysoxylum* spp.) are representative of core forest and thus may be indicators of the forest dynamics.

The ecological processes that drive the distribution and the dominance of species along the studied transects remained still unclear. Studying the species functional traits would help us to better understand the observed patterns of distribution (*e.g.* Maharjan *et al.* 2011; Müller *et al.* 2007) due to niche differentiation. Particularly, differences in functional traits related to fire (*e.g.* Hoffmann *et al.* 2003; Hoffmann and Solbrig 2003) and shade tolerance or photosynthetic capacity (*e.g.* Rossatto *et al.* 2009) and dispersal syndromes (*e.g.* Hovestadt *et al.* 1999) would help us to explain the distribution of species from savanna core to forest core. However, the drivers of the distribution and dominance of species belonging to both a same functional group and genus, such as *Cupaniopsis* spp. or *Dysoxylum* spp. (see Appendix III), would be more complex, ranging from the application of the niche theory to the application of the neutral one (Svenning *et al.* 2004).

10.6.2 Savanna-forest transition zone dynamics

Stem density, size distribution and species composition showed that the forest edge has likely shifted *ca* 40 m toward savanna during the last decades. The presence of a sharp boundary at the beginning of the savanna-forest transition zone, points out that the forest expansion has likely been stopped. Hence, as Banfai and Bowman (2007) in northern Australia, our results suggest that different phases may alternate in the savanna-forest transition zone dynamics; ‘stable’ phases where the transition zone does not move, and ‘instable’ phases where the transition zone moves or expands toward savanna (forest expansion) or forest (forest contraction).

Changes over ‘stable’ and ‘instable’ phases are likely due to changes in disturbance regime (intensity, season, extent, type and frequency, see Whelan 1995), which in turn affect the savanna-forest transition zone. This fire driven dynamic

hypothesis is in agreement with observations on worldwide savanna-forest transition zone dynamics. Indeed, it is widely observed that under temporary fire exclusion, such as abnormally moist condition and / or active fire suppression, forest can expand on savanna (e.g. Geiger *et al.* 2011; King *et al.* 1997; Russell-Smith *et al.* 2004b; Swaine *et al.* 1992). Inversely, under abnormally dry conditions (*e.g.* Alencar *et al.* 2004; Cochrane and Laurance 2002) and / or forest edge degradation due to logging and / or repeated fire (*e.g.* Barlow and Peres 2008; Cochrane *et al.* 1999; Didham and Lawton 1999), fires can penetrate in the forest understory, pushing the savanna-forest transition zone toward forest.

However, in 'normal' conditions, savannas fires do not penetrate in forest rather they sharpen the savanna-forest transition zone, which is traduce by a net boundary (see Ratnam *et al.* 2011). Indeed, in such conditions, on one hand, savanna fires prevent the establishment of forest trees in savanna as they are not fire tolerant (Gignoux *et al.* 2009; Hoffmann *et al.* 2003), and on the other hand, if the forest edge is closed enough, savannas fires do not penetrate in forest due low flammability and ignitability of forest fuels (Biddulph and Kellman 1998; Hennenberg *et al.* 2006). Fire regime may be affected by different or synergetic changes in vegetation, climate and ignition (Whelan 1995).

(i) *Vegetation changes*

Change in vegetation at the savanna-forest transition zone may affect its vulnerability to savanna fires. Forest expansion could make the boundary less vulnerable to fire over time and isolate the forest core from the surrounding savanna (Strayer *et al.* 2003). As mentioned above, the negative effect of forest edge degradation by logging (Cochrane 2003; Nepstad *et al.* 2001; Nepstad *et al.* 1999; Siegert *et al.* 2001), repeated fire (Balch *et al.* 2008; Cochrane 2003; Cochrane *et al.* 1999; Goldammer 1999) or windstorm (Laurance and Curran 2008) on fuel properties and fire behaviour is well documented. Inversely, the evolution of fuel loads and properties during forest secondary succession remained to our knowledge less studied in the tropics (but see Ray *et al.* 2005).

During forest expansion tree establishment reduces or suppresses the savanna grass layer, which in turn reduces fire frequency and intensity (Stott 2000). But one of

the critical remaining questions to understand savanna-forest transition zone dynamics is; when a forest stand is closed enough or a successional forest is advanced enough to present micro-climatic condition and fuel properties that prevent forest from fire? A companion study, performed on the same transects has shown that at least during relatively humid years, the recovering forest had the same micro-climatic conditions (air temperature, relative humidity and vapour deficit pressure) as the forest core, while the most important change was located in the savanna close to the forest edge.

The invasion by weeds may be also an important driver of the savanna-forest transition zone dynamics as they conduce to dramatic change in the grass layer composition. Indeed, weeds alters fuel load and properties, which in turn affect fire regime (Mistry and Berardi 2005; Stott 2000) and the vulnerability to fire of savanna-forest boundary (Hoffmann *et al.* 2004) but also limit tree establishment and forest expansion (*e.g.* Hoffmann and Haridasan 2008; Ortega-Pieck *et al.* 2011).

(ii) *Climate changes*

Climate is one of the main drivers of fire regime (Whelan 1995) and at large spatial and temporal scales, change in temperature and / or rainfall drive savanna-forest boundary (Banfai and Bowman 2006; Banfai and Bowman 2007; Beerling and Osborne 2006; Bond 2008). Hence, at the decadal scale, the dynamic of the savanna-forest transition zone may be linked to change over abnormal humid periods and abnormal drought periods. In New Caledonia (Barbero *et al.* in press.; Nicet and Delcroix 2000), as in many places in the tropics (Alencar *et al.* 2004; Fuller and Murphy 2006; Le Page *et al.* 2008; Siegert *et al.* 2001; van der Werf *et al.* 2008b), these change are likely due to the El Niño Southern Oscillation (ENSO) phenomenon.

In the tropics, although the occurrence of fire is closely linked with the length and the intensity of the dry season, the relationship between climate and fire regime is not straightforward (van der Werf *et al.* 2008b). Indeed, climate affects both fuel load and moisture. Hence, in savannas, while long and intense dry seasons may promote fire by decreasing fuel moisture, low rainfalls during the fuel load production may limit fuel availability, fire frequency and intensity (Hély and Alleaume 2006; van der Werf *et al.* 2008b).

Vegetation also affects the micro-climatic condition, closed forest edge isolating forest interior from the drier condition in the surrounding savanna (Ibanez *et al.* in prep.-b). Inversely, forest trees shade the savanna closed to the forest edge offering moister conditions for the establishment and the growth of forest trees and isolating the forest edge from fire with a moister and thus less flammable zone (Biddulph and Kellman 1998; Hennenberg *et al.* 2006). Ecologists have unfortunately less studied such savanna side edge effects than forest side ones (Fonsca and Joner 2007), however we suggest that their strength have critical importance in the dynamics of the savanna-forest transition zone.

(iii) *Ignition changes*

As many places in the tropics (Stott 2000), Humans are by far the first source of ignition in New Caledonia. Generally, fires are lighted in open areas (see Ibanez *et al.* submitted-b, for more details on fire practices) and spread into savanna until a forest edge is encountered (Tinquaut et al. in. prep. ; Curt et al. in. prep.). Given that, land use and fire practices in the neighbourhood of a savanna-forest boundary are likely the main drivers of its dynamics. Hence, understanding the impacts of socio-environmental changes on fire practices is critical for landscape management and forest conservation.

For instance, around the *Aoupinié* mountain, where this study took placed, the rainforest globally has been regressing in the vicinity of the tribe of *Gohapin* for the last five decades (Ibanez *et al.* submitted-b), while it has been expanding in the vicinity of the tribe of *Pöö*. These different dynamics are likely due to an intensive use of fire by people in *Gohapin* associated to new fire use practices (Ibanez *et al.* submitted-b), while in *Pöö* the use of fire is declining (Toussaint pers. com.).

10.6.3 Conclusion

Our results support the complexity of the structure and the composition of transitional zones between savanna and rainforest and point out the need of multivariate analyses to fully understand their dynamics. We suggest through the analysis of several vegetation statistics that the dynamic of such transitional zones is likely characterised by an

alternation of 'stable' and 'instable' phases, which switch from one to the other according to fire regime. The El Niño phenomenon interacting with human fire use, land use and vegetation changes, likely drive this dynamic.

10.7 Acknowledgments

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10.8 Appendix

Appendix I *Number of individuals per species inventoried along the three transects. For each species and families, the total number of inventoried inviduals is also given in percentage of the total inventoried individuals. For the species statut, EE refers to endemic genus, E to endemic species, A to autochthonous species and I to introduced species Letters indicate if the species has been classified as savanna species (S = M. quinquenervia + 'pioneer' group), ecotone species (E = 'post-pioneer' group) or forest species (F = 'forest' group) by the DCAs in the three transects separately.*

Family	Taxon	Statut	T1	T2	T3	Total (%)
Anacardiaceae	*Semecarpus atra* (G. Forst.) Vieill.	E	0	0	1	1 (0.1)
Annonaceae	*Polyalthia nitidissima* (Dunal) Benth.	A	0	1	0	1 (0.1)
Apocynaceae	*Alstonia costata* (G.Forst.) R.Br.	A	3	2	4	9 (0.5)
	Alstonia sp.	A	1	1	0	2 (0.1)
	Tabernaemontana cerifera Pancher & Sebert	E	0	1	6 (F)	7 (0.4)
						18 (1.0)
Aquifoliaceae	*Ilex sebertii* Pancher & Sebert	E	1	3	0	4 (0.2)

Araliaceae	*Meryta balansae* Baill.	E	2	2	6 (S)	10	(0.5)
	Meryta oxylaena Baill.	E	1	1	0	2	(0.1)
	Plerandra gabriellae (Baill.) Lowry, G.M.Plunkett & Frodin ined.	E	40 (E)	7 (S)	29 (S)	76	(4.2)
	Plerandra gpe *candelabra/pseudocandelabra*	E	1	0	1	2	(0.1)
	Plerandra leptophylla (Veitch ex T. Moore) Lowry, G.M.Plunkett & Frodin ined.	E	1	1	0	2	(0.1)
	Plerandra osyana subsp. *toto* (Baill.) Lowry, G.M.Plunkett & Frodin comb. ined.	E	0	0	6 (E)	6	(0.3)
	Plerandra pancheri (Baill.) Lowry, G.M.Plunkett & Frodin	E	0	4	1	5	(0.3)
	Plerandra sp.	E	0	1	1	2	(0.1)
	Polyscias bracteata subsp. *bracteata* (R.Vig.) Lowry	E	0	0	1	1	(0.1)
	Schefflera sp.	E	2	5 (S)	4	11	(0.6)
						117	**(6.4)**
Araucariaceae	*Agathis* sp.	E	1	0	0	1	(0.1)
Arecaceae	*Burretiokentia vieillardii* (Brongn. & Gris) Pic. Serm.	E	0	0	6 (F)	6	(0.3)
Asparagaceae	*Cordyline* sp.	A	1	0	0	1	(0.1)
Bignoniaceae	*Deplanchea speciosa* Vieill.	E	0	2	0	2	(0.1)

Calophyllaceae	*Calophyllum caledonicum* Vieill. ex Planch. & Triana	E	2	0	3	5	(0.3)
Clusiaceae	*Garcinia neglecta* Vieill.	E	5 (F)	2	0	7	(0.4)
	Garcinia puat Guillaumin	E	2	5 (F)	10 (F)	17	(0.9)
	Garcinia sp. (JM4818)	E	3	0	0	3	(0.2)
	Montrouziera cauliflora Planch. & Triana	E	1	0	0	1	(0.1)
						28	**(1.5)**
Corynocarpaceae	*Corynocarpus* sp.	E	0	0	2	2	(0.1)
Cunoniaceae	*Cunonia* sp.	A	0	1	0	1	(0.1)
	Geissois balansae Brongn. & Gris ex Guillaumin	E	5 (F)	1	5 (S)	11	(0.6)
	Geissois racemosa Labill.	E	2	1	6 (E)	9	(0.5)
	Geissois sp.	E	0	0	11 (S)	11	(0.6)
	Pancheria ternata Brongn. & Gris	E	5 (F)	1	0	6	(0.3)
	Spiraeanthemum densiflorum Brongn. & Gris	E	2	1	0	3	(0.2)
	Weinmannia serrata Brongn. & Gris	E	21 (S)	31 (E)	8 (S)	60	(3.3)
						101	**(5.5)**
Cyatheaceae	*Alsophila vieillardii* (Mett.) R.M.Tryon	A	0	0	1	1	(0.1)

	Sphaeropteris intermedia (Mett.) R.M.Tryon	E	0	0	1	1	(0.1)
	Sphaeropteris novae-caledoniae (Mett.) R.M.Tryon	E	1	2	0	3	(0.2)
						5	**(0.3)**
Dicksoniaceae	*Dicksonia thyrsopteroides* Mett.	E	67 (S)	68 (E)	25 (S)	160	(8.8)
Dilleniaceae	*Hibbertia* sp.	E	0	1	0	1	(0.1)
Ebenaceae	*Diospyros fasciculosa* (F. Muell.) F. Muell.	A	0	1	9 (F)	10	(0.5)
	Diospyros macrocarpa Hiern	E	0	1	7 (F)	8	(0.4)
	Diospyros olen Hiern	A	2	0	0	2	(0.1)
	Diospyros sp.	E	0	0	1	1	(0.1)
	Diospyros trisulca F.White	E	0	1	0	1	(0.1)
						22	**(1.2)**
Elaeocarpaceae	*Elaeocarpus* sp.	E	0	1	0	1	(0.1)
	Sloanea ramiflora Tirel	E	0	0	1	1	(0.1)
						2	(0.1)
Euphorbiaceae	*Codiaeum peltatum* (Labill.) P.S.Green	A	4	0	3	7	(0.4)

	Euphorbiaceae sp.	A	0	0	1	1	(0.1)
						8	**(0.4)**
Fabaceae	*Intsia bijuga* (Colebr.) Kuntze	A	0	0	1	1	(0.1)
	Archidendropsis fournieri var. *auriculata* (Charpent. ex Fourn.) I.C.Nielsen	E	0	0	1	1	(0.1)
	Archidendropsis sp.	E	0	5 (F)	0	5	(0.3)
	Archidendropsis streptocarpa (E. Fourn.) I.C.Nielsen	E	0	2	0	2	(0.1)
						9	**(0.5)**
Flacourtiaceae	*Xylosma confusum* Guillaumin	E	0	0	5 (S)	5	(0.3)
	Xylosma sp.	E	10 (E)	2	0	12	(0.7)
						17	**(0.9)**
Gentianaceae	*Fagraea berteroana* A.Gray ex Benth.	A	6 (E)	15 (S)	5 (S)	26	(1.4)
	Depanthus glaber (C.B.Clarke) S.Moore	E	0	0	2	2	(0.1)
						28	**(1.5)**
Goodeniaceae	*Scaevola cylindrica* Schltr.	A	0	0	2	2	(0.1)
Hernandiaceae	*Hernandia cordigera* Vieill.	E	1	0	0	1	(0.1)

Lamiaceae	*Oxera coronata* de Kok	E	1	0	1	2	(0.1)
	Oxera robusta Vieill.	E	1	1	0	2	(0.1)
	Oxera sp.	A	1	1	4	6	(0.3)
						10	**(0.5)**
Lauraceae	*Cryptocarya aristata* Kosterm.	E	0	1	0	1	(0.1)
	Cryptocarya elliptica Schltr.	E	2	2	1	5	(0.3)
	Cryptocarya oubatchensis Schltr.	E	0	0	1	1	(0.1)
	Cryptocarya pluricostata Kosterm.	E	1	6 (F)	1	8	(0.4)
	Cryptocarya sp. (JM5874)	E	0	1	0	1	(0.1)
	Cryptocarya sp. (JM5178)	E	1	3	0	4	(0.2)
	Cryptocarya velutinosa Kosterm.	E	1	1	0	2	(0.1)
						22	**(1.2)**
Loganiaceae	*Geniostoma erythrospermum* Baill.	E	0	1	0	1	(0.1)
	Geniostoma sp.	A	0	0	1	1	(0.1)
	Neuburgia neocaledonica (Gilg & Benedict) J.Molina & Struwe	A	0	0	4	4	(0.2)
						6	**(0.3)**

Lomariopsidaceae	*Teratophyllum wilkesianum* (Brackenr.) Holttum	A	0	0	1	1	(0.1)
Meliaceae	*Anthocarapa nitidula* (Benth.) T.D.Penn. ex Mabb.	A	3	2	0	5	(0.3)
	Dysoxylum sp.	A	2	2	26 (E)	30	(1.6)
	Dysoxylum kouiriense Virot	E	4	5 (F)	3	12	(0.7)
	Dysoxylum macranthum C.DC.	E	0	3	40 (F)	43	(2.4)
	Dysoxylum macrostachyum C.DC.	E	1	16 (F)	0	17	(0.9)
	Dysoxylum roseum C.DC.	E	8 (F)	8 (F)	0	16	(0.9)
	Dysoxylum rufescens subsp. *dzumacense* (Guillaumin) Mabb.	E	59 (F)	77 (F)	0	136	(7.5)
						259	**(14.2)**
Monimiaceae	*Hedycarya chrysophylla* Perkins	E	0	0	2	2	(0.1)
	Hedycarya cupulata Baill.	E	35 (F)	24 (F)	10 (E)	69	(3.8)
	Hedycarya engleriana S.Moore	E	3	3	3	9	(0.5)
	Hedycarya sp.	E	1	1	1	3	(0.2)
						83	**(4.6)**
Moraceae	*Ficus habrophylla* Bennett ex Seemann	A	0	3	1	4	(0.2)
	Ficus leiocarpa (Bureau) Warb.	E	0	0	1	1	(0.1)
	Ficus racemigera Bureau	E	4	3	5 (F)	12	(0.7)

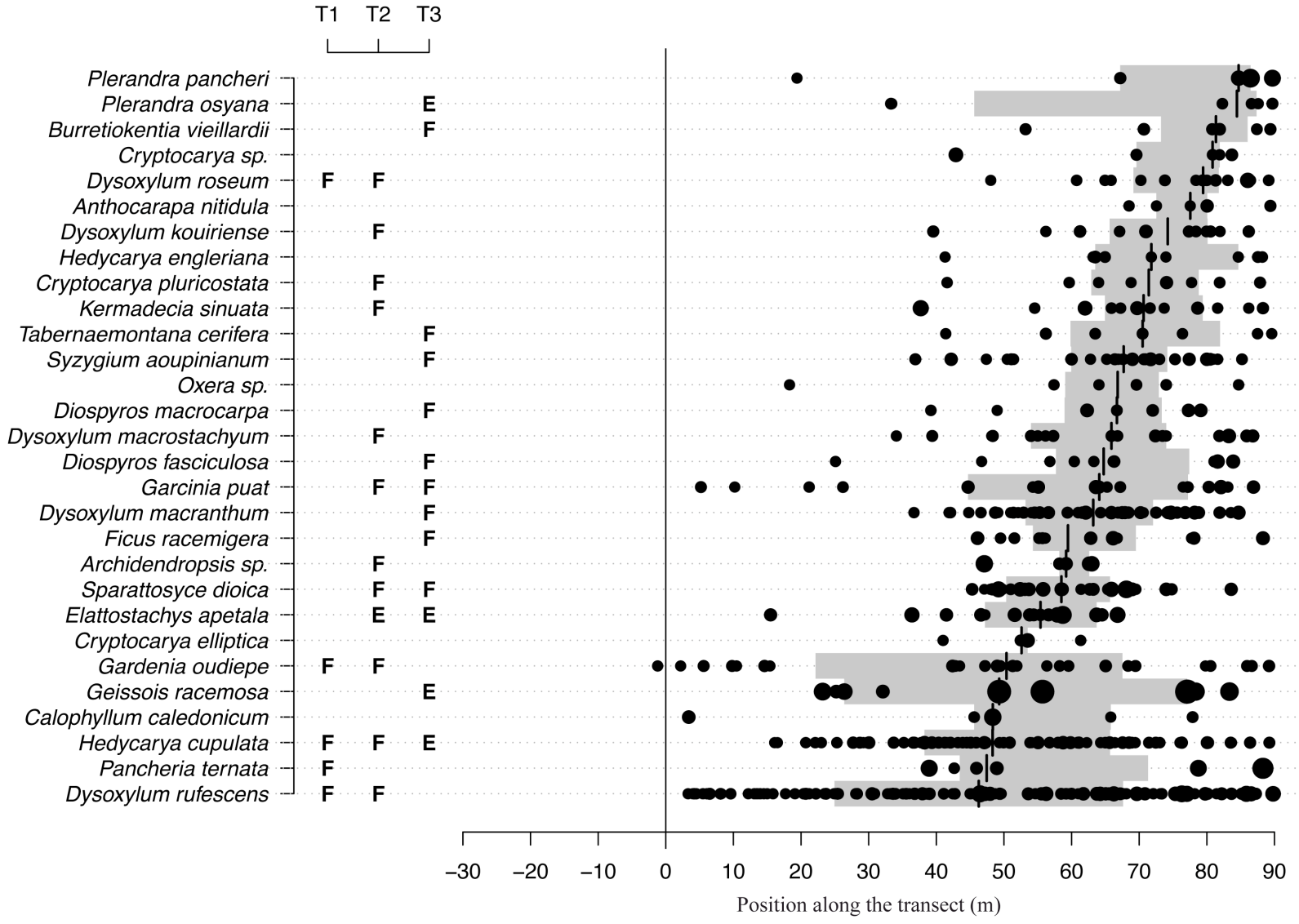
	Ficus versicolor Bureau	E	0	0	2	2	(0.1)
	Ficus vieillardiana Bureau	E	0	1	0	1	(0.1)
	Sparattosyce dioica Bureau	E	0	20 (F)	15 (F)	35	(1.9)
						55	**(3.0)**
Myodocarpaceae	*Myodocarpus pinnatus* Brongn. & Gris	E	6 (E)	6 (F)	3	15	(0.8)
Myrtaceae	*Eugenia* sp.	A	0	0	1	1	(0.1)
	Melaleuca quinquenervia (Cav.) S.T.Blake	A	69 (S)	75 (S)	76 (S)	220	(12.1)
	Myrtaceae sp.	E	5 (E)	2	0	7	(0.4)
	Piliocalyx laurifolius Brongn. & Gris	E	2	0	0	2	(0.1)
	Piliocalyx wagapensis Brongn. & Gris	E	0	0	3	3	(0.2)
	Syzygium aoupinianum J.W.Dawson	E	0	1	26 (F)	27	(1.5)
	Syzygium densiflorum Brongn. & Gris	E	0	1	0	1	(0.1)
						261	**(14.3)**
Oleaceae	*Chionanthus brachystachys* (Schltr.) P.S.Green	A	0	0	1	1	(0.1)
	Olea paniculata R.Br.	A	0	0	3	3	(0.2)
						4	**(0.2)**

Phyllanthaceae	*Bischofia javanica* Blume	A	0	0	1	1	(0.1)
	Glochidion billardierei Baill.	E	13 (E)	7 FB)	1	21	(1.2)
						22	**(1.2)**
Piperaceae	*Macropiper* sp.	A	0	0	3	3	(0.2)
Primulaceae	*Maesa novocaledonica* Mez	E	0	1	0	1	(0.1)
	Rapanea discocarpa M.Schmid	E	0	0	2	2	(0.1)
	Rapanea modesta Mez	A	4	3	0	7	(0.4)
	Rapanea sp.	A	0	1	0	1	(0.1)
						11	**(0.6)**
Proteaceae	*Kermadecia sinuata* Brongn. & Gris	E	2	6 (F)	4	12	(0.7)
	Stenocarpus trinervis (Montr.) Guillaumin	E	0	1	0	1	(0.1)
						13	**(0.7)**
Rhizophoraceae	*Crossostylis grandiflora* Pancher ex Brongn. & Gris	E	0	0	4	4	(0.2)
	Crossostylis multiflora Brongn. & Gris	E	39 (S)	32 (E)	16 (S)	87	(4.8)
						91	**(5.0)**

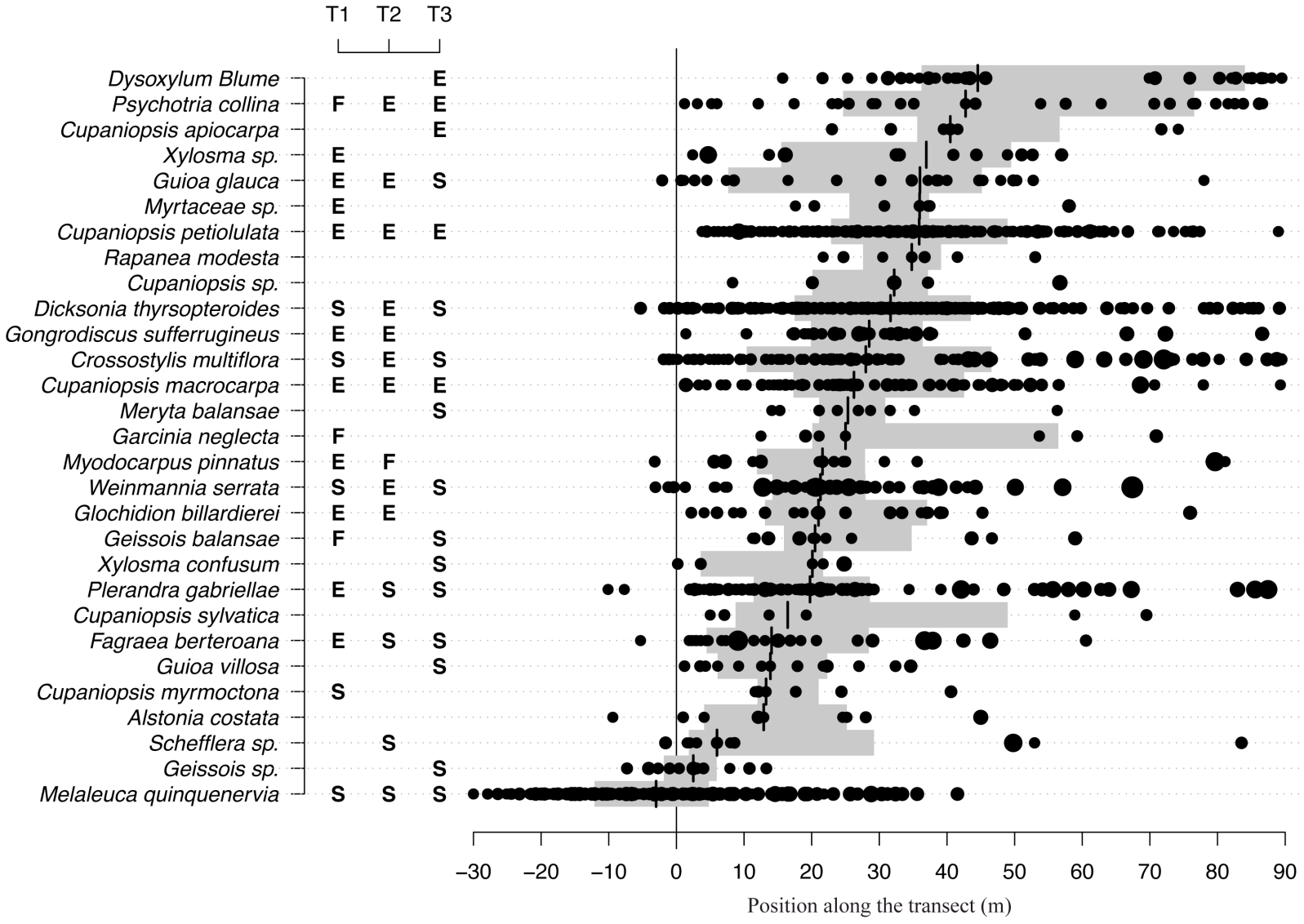
Rubiaceae	*Aidia vieillardii* (Baill.) Ridsdale	E	0	3	0	3	(0.2)
	Gardenia oudiepe Vieill.	E	15 (F)	8 (F)	3	26	(1.4)
	Psychotria collina Labill.	A	17 (F)	9 (E)	5 (E)	31	(1.7)
						60	**(3.3)**
Rutaceae	*Acronychia laevis* J.R.Forst. & G.Forst.	A	2	0	0	2	(0.1)
	Comptonella drupacea (Labill.) Guillaumin	E	0	1	2	3	(0.2)
	Comptonella oreophila var. *longipes* (Guillaumin) T.G.Hartley	E	0	1	0	1	(0.1)
						6	**(0.3)**
Sapindaceae	*Cupaniopsis apiocarpa* Radlk.	E	0	1	6 (E)	7	(0.4)
	Cupaniopsis chytradenia Radlk.	E	0	0	1	1	(0.1)
	Cupaniopsis macrocarpa var. *macrocarpa* Radlk.	E	23 (E)	30 (E)	5 (E)	58	(3.2)
	Cupaniopsis macrocarpa var. *polyphylla* Adema	E	5 (E)	3	0	8	(0.4)
	Cupaniopsis myrmoctona Radlk.	E	5 (S)	2	1	8	(0.4)
	Cupaniopsis petiolulata Radlk.	E	59 (E)	53 (E)	26 (E)	138	(7.6)
	Cupaniopsis sp.	A	1	3	2	6	(0.3)
	Cupaniopsis sylvatica Guillaumin	E	1	4	1	6	(0.3)
	Elattostachys apetala (Labill.) Radlk.	A	0	5 (E)	13 (E)	18	(1.0)
	Gongrodiscus sufferrugineus Radlk.	E	10 (E)	18 (E)	3	31	(1.7)

	Guioa glauca (Labill.) Radlk.	E	7 (E)	10 (E)	5 (S)	22	(1.2)
	Guioa ovalis Radlk.	A	0	2	1	3	(0.2)
	Guioa sp.	E	0	0	3	3	(0.2)
	Guioa villosa Radlk.	E	1	0	12 (S)	13	(0.7)
	Harpullia austrocaledonica Baill.	E	2	0	2	4	(0.2)
	Podonephelium pachycaule Munzinger, Lowry, Callm. & Buerki ined.	E	1	1	2	4	(0.2)
	Sapindaceae sp.	E	0	1	0	1	(0.1)
						331	**(18.2)**
Sapotaceae	*Pycnandra balansae* (Baill.) Swenson & Munzinger	E	0	0	2	2	(0.1)
Symplocaceae	*Symplocos arborea* (Vieill.) Brongn. & Gris	E	0	0	1	1	(0.1)
	Symplocos montana var. *tortuosa* (Vieill. ex Guillaumin) Noot.	E	2	1	0	3	(0.2)
						4	**(0.2)**
Not-identified			7	8	5	20	(1.1)
Total			619	658	544	1821	-

Appendix II (next pages) *Locations of the individuals species inventoried with 5 or more individuals along the transects. Black circles represent trees (the diameters of the circles is proportional the DBH of the trees), greys areas represent the first and fourth quartiles intervals and the bold vertical lines represent the medians. Letters indicate if the species has been classified as savanna species (S = M. quinquenervia + 'pioneer' group), ecotone species (E = 'post-pioneer' group) or forest species (F = 'forest' group) by the DCAs in the three transects separately.*

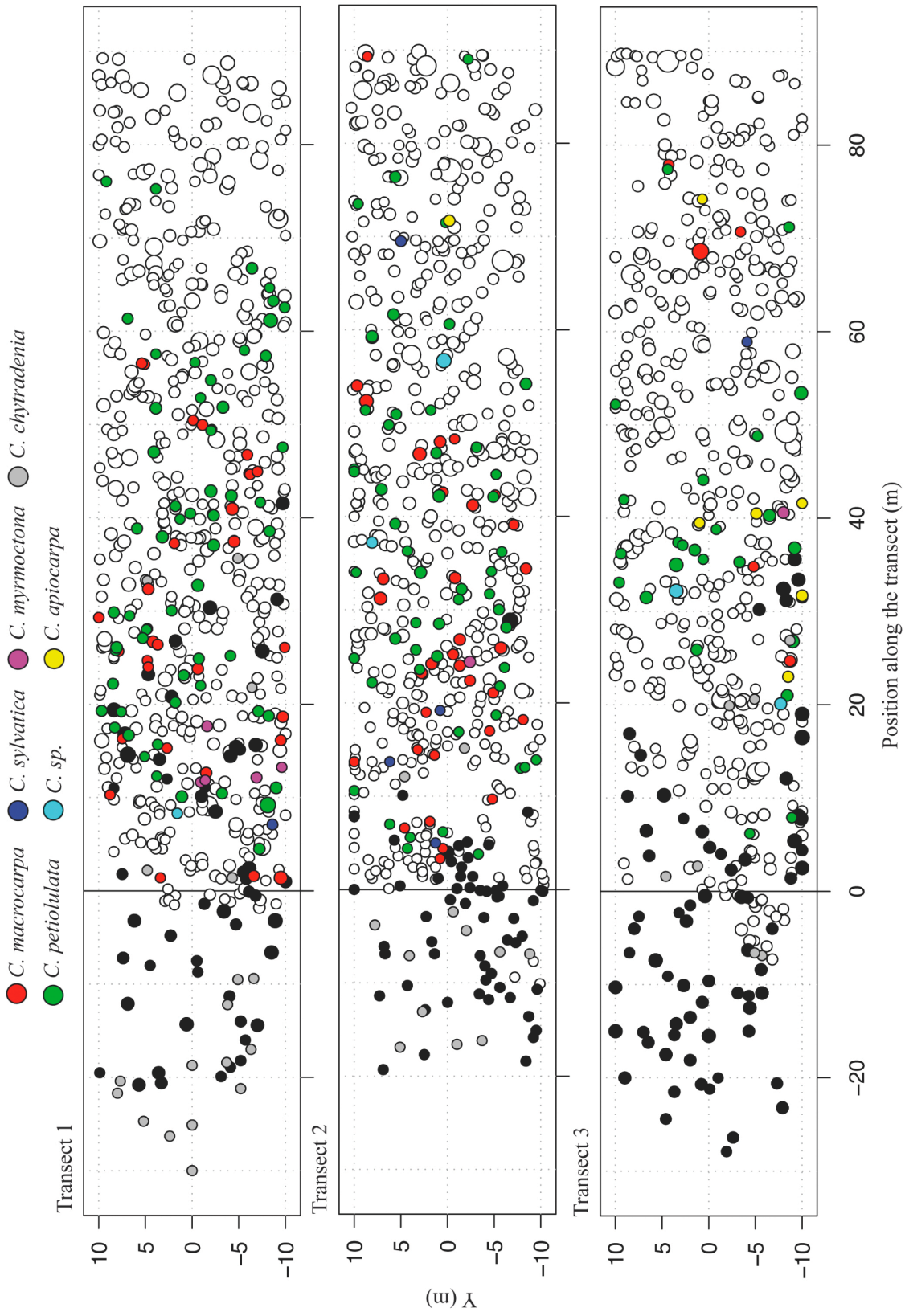

T1
T2
T3
Plerandra pancheri
Plerandra osyana E
Burretiokentia vieillardii F
Cryptocarya sp.
Dysoxylum roseum F F
Anthocarapa nitidula
Dysoxylum kouiriense F
Hedycarya engleriana
Cryptocarya pluricostata F
Kermadecia sinuata F
Tabernaemontana cerifera F
Syzygium aoupinianum F
Oxera sp.
Diospyros macrocarpa F
Dysoxylum macrostachyum F
Diospyros fasciculosa F
Garcinia puat F F
Dysoxylum macranthum F
Ficus racemigera F
Archidendropsis sp. F
Sparattosyce dioica F F
Elattostachys apetala E E
Cryptocarya elliptica
Gardenia oudiepe F F
Geissois racemosa E
Calophyllum caledonicum
Hedycarya cupulata F F E
Pancheria ternata F
Dysoxylum rufescens F F
−30 −20 −10 0 10 20 30 40 50 60 70 80 90
Position along the transect (m)

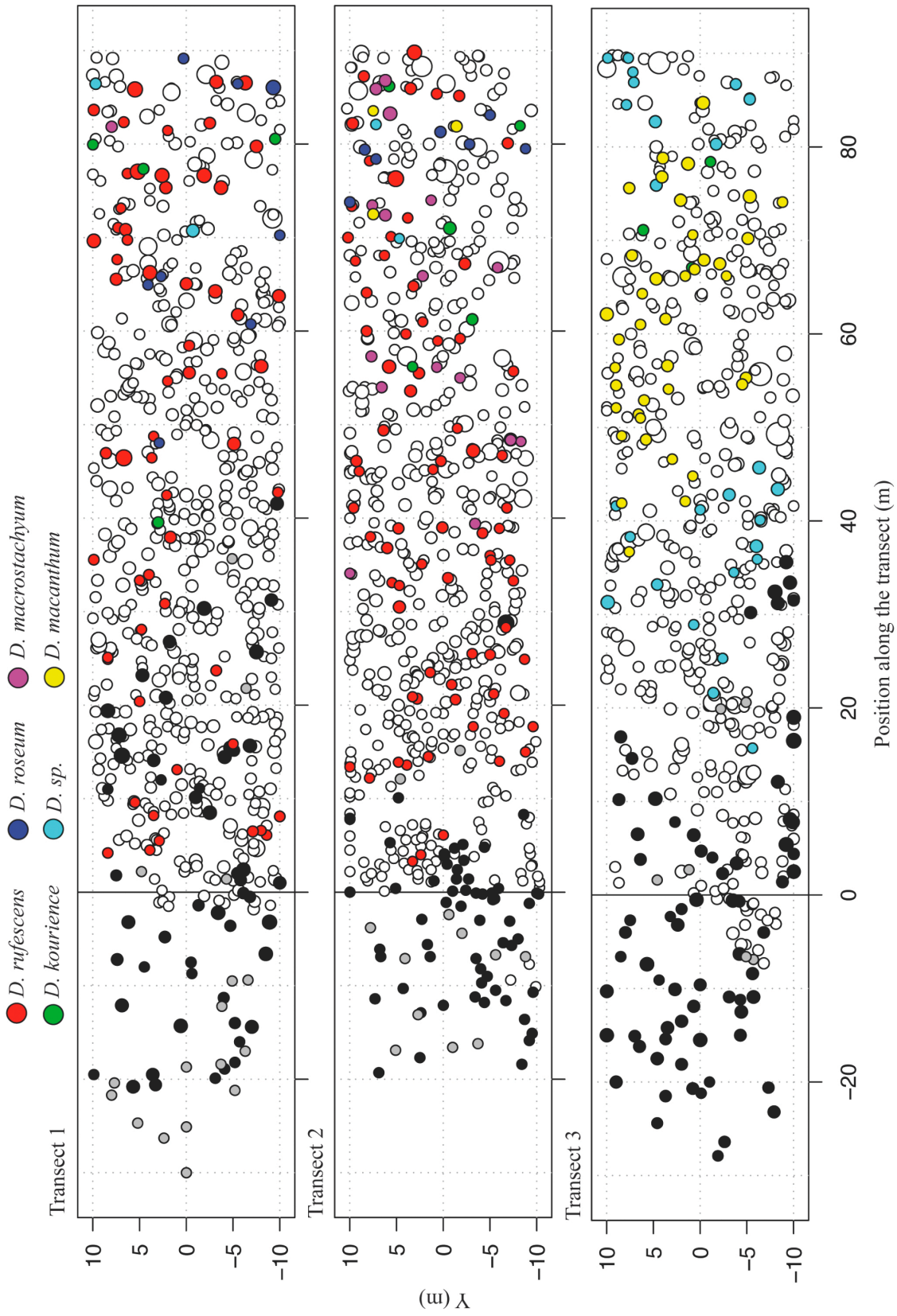
(Part 1)


T1
T2
T3
Dysoxylum Blume E
Psychotria collina F E E
Cupaniopsis apiocarpa E
Xylosma sp. E
Guioa glauca E E S
Myrtaceae sp. E
Cupaniopsis petiolulata E E E
Rapanea modesta
Cupaniopsis sp.
Dicksonia thyrsopteroides S E S
Gongrodiscus sufferrugineus E E
Crossostylis multiflora S E S
Cupaniopsis macrocarpa E E E
Meryta balansae S
Garcinia neglecta F
Myodocarpus pinnatus E F
Weinmannia serrata S E S
Glochidion billardierei E E
Geissois balansae F S
Xylosma confusum S
Plerandra gabriellae E S S
Cupaniopsis sylvatica
Fagraea berteroana E S S
Guioa villosa S
Cupaniopsis myrmoctona S
Alstonia costata
Schefflera sp. S
Geissois sp. S
Melaleuca quinquenervia S S S
−30 −20 −10 0 10 20 30 40 50 60 70 80 90
Position along the transect (m)

(Part II)

Appendix III *(next pages) Maps of Cupaniopsis spp. (1st page) and Dysoxylum spp. (2nd page). Black and grey circles represent Melaleuca quinquenervia alive and dead trees, respectively and white ones represent others forest tree species. The diameters of the circles are proportional the DBH of the trees. The black vertical line represents the forest edge as determined on the field.*


C. macrocarpa
C. petiolulata
C. sylvatica
C. sp.
C. myrmoctona
C. apiocarpa
C. chytradenia
Transect 1
Transect 2
Transect 3
Y (m)
Position along the transect (m)


D. rufescens
D. kourrience
D. roseum
D. sp.
D. macrostachyum
D. macanthum
Transect 1
Transect 2
Transect 3
Y (m)
Position along the transect (m)

11 Sharp transition of microclimatic conditions between savanna and rainforest in New Caledonia: insights for rainforest edge vulnerability to fire

This section is in preparation for submition to *Journal of Tropical Ecology* as the following research paper :

Ibanez, T., Gaucherel, C., and Hély, C., (in prep.). Sharp transition of microclimatic conditions between savanna and rainforest in New Caledonia: insights for rainforest edge vulnerability to fire, in preparation for submition to *Journal of Tropical Ecology*.

11.1 Résumé

Dans les paysages forestiers fragmentés, les fragments de forêt entourés par une matrice de biomasse et de complexité structurelle plus faible tels que les savanes, sont affectés par des effets de bord microclimatiques. Ces effets de bord peuvent dessécher la lisière de la forêt et augmenter sa vulnérabilité aux incendies se propageant dans la matrice environnante. Dans cette étude, nous avons mesuré et analysé les variations des conditions microclimatiques (température, humidité relative et déficit de pression de vapeur de l'air) durant sept mois le long de trois transects allant de l'intérieur de la savane à celui de la forêt. Nous avons testé les hypothèses selon lesquelles, (i) la lisière de la forêt est soumise à des effets de bord microclimatiques tels que la dessiccation de son sous bois, et (ii) que la profondeur de ces effets de bord augmente pendant les périodes sèches. Contrairement à ce à quoi nous nous attendions, la transition des conditions microclimatiques entre la savane et la forêt a été très abrupte tout au long de la période étudiée (environ 5m) et a été situé à l'extérieur de la forêt. Nous suggérons que ces résultats sont liés au fait que l'année étudiée était anormalement humide (épisode *La Niña*), et que dans de telles conditions la vulnérabilité de la lisière forestière aux feux de savane est relativement faible, alors que les conditions plus humides le long de la lisière forestière an savane pourraient favoriser l'expansion de la forêt. Enfin, durant les périodes anormalement sèches (*El Niño*), la zone de transition des conditions microclimatiques entre la savane et la forêt devrait se décaler vers l'intérieur de la forêt, ce qui dessécherait le sous-bois et rendrait la lisière forestière plus vulnérable aux feux de savanes. Des brûlages dirigés au cours des années humides pourrait limiter l'accumulation de combustibles en savane sans pour autant affecter la lisière forestière, et ainsi la prévenir d'impacts plus dramatiques lors d'incendies durant les années sèches.

Mots-clés: deficit de pression vapeur, ecotone, effets de bord, humidité relative, sous-bois forestier, température.

11.2 Abstract

In fragmented forested landscapes, forest fragments surrounded by a matrix of lower biomass and structural complexity such as savanna are affected by microclimatic edge effects. Such edge effects may dry the forest edge, which increase its vulnerability to fire that spread in the surrounding matrix. In this study, we measured and analysed the variation of microclimatic conditions (air temperature, relative humidity and vapour deficit pressure) during seven months along three transects from savanna to rainforest interiors. We test the hypotheses that, (i) the forest edge is submitted to climatic edge effects such as its understory desiccation, and (ii) that the depth of these edge effects increases during dry periods. Contrarily to what we expected, the transition of microclimatic conditions between savanna and forest was very sharp all over the studied period (ca. 5m) and was situated outside forest. We suggest that these results were linked to the fact that the studied year was abnormally humid (*La Niña* episode), and that in such conditions the vulnerability of the forest edge to savanna fires is relatively low while the moister condition in savanna close to the forest edge may promote forest expansion. Finally, during abnormally dry periods (*El Niño* episodes), the transition zone between savanna and rainforest microclimatic conditions would shift toward forest interior drying the understory and making the forest edge more vulnerable to savannas fire. Prescribed fires during humid years would limit the fuel load accumulation in savanna without affecting the forest edge, which would prevent dramatic fire impacts during dry years.

Keywords: ecotone, edge effects, forest understory, relative humidity, temperature, vapour deficit pressure.

11.3 Introduction

In fragmented forested landscapes, forest fragments surrounded by a matrix of lower biomass and structural complexity such as pasture or savanna may be affected by edge effects (Fonsca and Joner 2007; Murcia 1995). Such edge effects resulting from the interaction between two adjacent ecosystems encompass (i) abiotic effects such as change in microclimatic conditions, (ii) direct biotic effects such as change in species composition and, (iii) indirect biotic effects, which involve change in species interaction such as seed dispersal by birds (Murcia 1995). Microclimatic edge effects and particularly forest edge desiccation have strong implication in forest edge vulnerability to fire occurring in the surrounding matrix (Cochrane 2003; Cochrane and Laurance 2002).

The erosion of fragmented forest edges promoted by edge effect is one of the main causes of forest loss in the tropics (Cochrane 2003; Goldammer 1999; Nepstad *et al.* 1999). Flammability of rainforests is relatively low and fires first occurring in forests typically propagate slowly, they are low in intensity and do not penetrate deep in the forest understory (Cochrane *et al.* 1999). However, these first fires (and/or tree logging) modify edge structure, fuel composition and microclimatic conditions, which facilitate the propagation of subsequent fires, increasing therefore the vulnerability of forest stands to future fires (Barlow and Peres 2008; Cochrane *et al.* 1999; Siegert *et al.* 2001) although a short period of lower flammability may also occur after a fire due to the absence of litter fuels (Balch *et al.* 2008).

In the New Caledonian biodiversity hotspot (Mittermeier *et al.* 2004; Myers 2003), more than the half of the original vegetation has already been destroyed and replaced by anthropogenic formations along the past centuries mainly due to fires, mining and logging (Jaffré *et al.* 1998). On volcano-sedimentary substrate rainforest has been mostly replaced by savannas. As a result at middle elevations the landscape is composed of a mosaic of savanna and rainforest (e.g. Ibanez *et al.* submitted-b).

Anthropogenic fires are considered as one of the major threats for the New Caledonian rainforest and terrestrial biodiversity (Jaffré *et al.* 1998; Pascal *et al.* 2008). Indeed, it has long been suggested that anthropogenic fires ignited in open areas such as savanna erode the forest edge (Jaffré *et al.* 1997b). This hypothesis has been recently

reinforced by remote sensing analysis of fires (Curt, *et al.* in prep) or vegetation (Ibanez *et al*. submitted), and fire modelling analysis (Tinquaut, *et al.* in prep.). However the processes that allow savanna fire to erode forest edge, are poorly known.

We hypothesise that microclimatic edge effects dry the forest edge understory allowing savanna fire to penetrate in the forest and erode it. In this study we analysed the variation of microclimatic conditions along transects from savanna to rainforest interiors. We test the hypotheses that (i) the forest edge is submitted to climatic edge effects such as edge desiccation and (ii) that the depth of these edge effects increases during dry periods. Then we discuss our results in terms of vulnerability of rainforest edges to savanna fires.

11.4 Materials and methods

11.4.1 Sampling for microclimatic conditions

In order to measure microclimatic variations from savanna to forest interiors we measured air temperature (T°C) and relative humidity (RH in %) using data-loggers (HOBO Pro-V2 U23) along three transects (described in the Ibanez *et al.* in prep.-c). We positioned 12 data-loggers along each transect ; three in savanna, one on the savanna-forest boundary and eight in forest (Figure 11.1). Data-loggers were denser close to the savanna-forest boundary in order to better characterize the transition in microclimatic conditions. Data loggers were placed on 1-m high poles and shielded from radiations and rainfalls to avoid bias (see Figure 11.2). T and RH were measured over 212 days every 20 min from April 04th 2010 (Julian day 94) to November 1st 2010 (Julian day 305). This period overlapped the expected dry season, which started in August (Julian day 212) and finished in late November (METEO-France 2007).

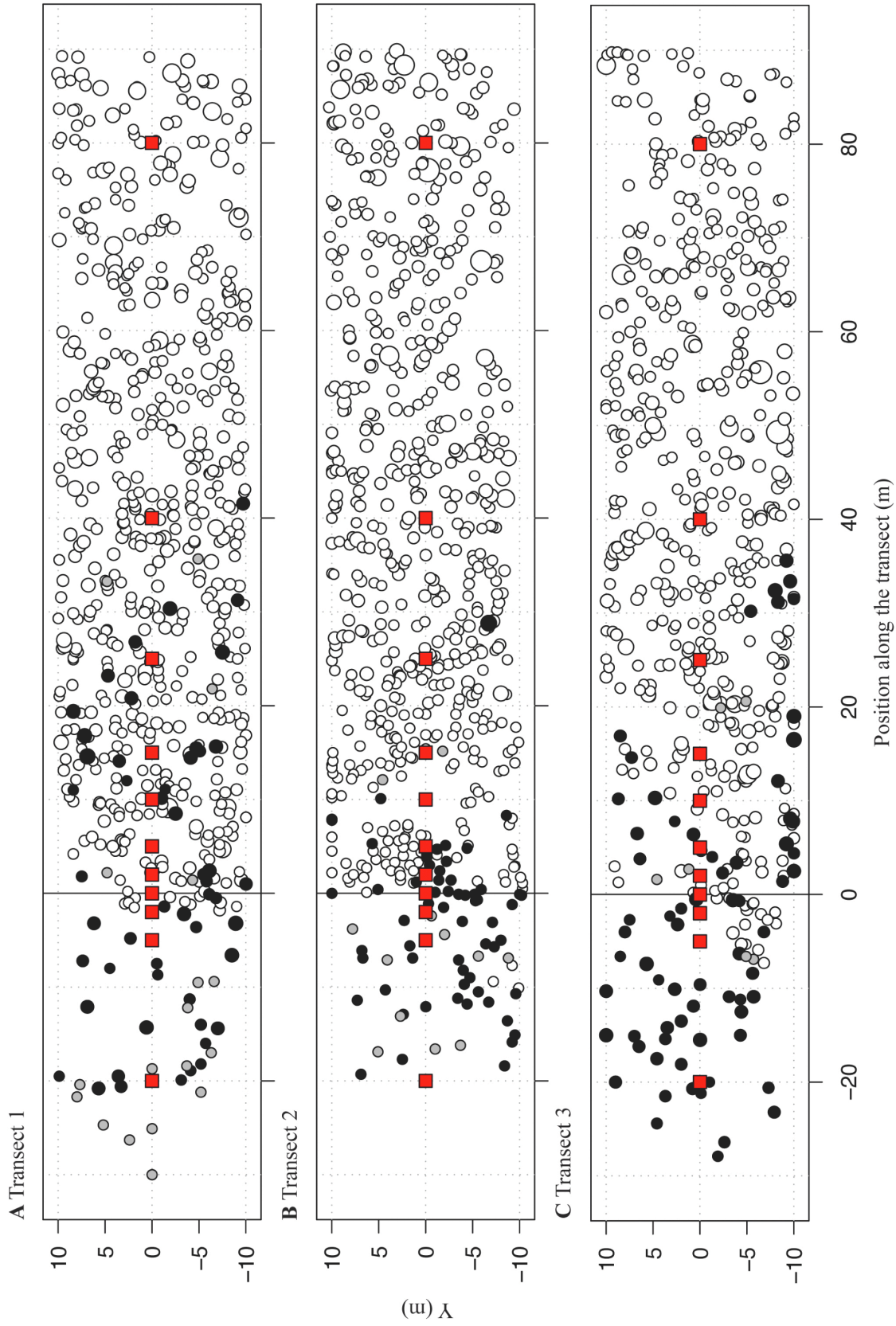

A Transect 1
B Transect 2
C Transect 3
Y (m)
10
5
0
−5
−10
−20
0
20
40
60
80
Position along the transect (m)

Figure 11.1 *(previous page) Positions of the microclimatic stations (red square) along the three studied transects (in savanna at -20, -5 and -2 m, on the boundary at 0 m and in forest at 2, 5, 10, 15, 25, 40, 60 and 80 m). Black and grey circles represent Melaleuca quinquenervia alive and dead trees, respectively, and white ones represent other trees species. The circle diameters are proportional to the tree DBH. The black vertical line represents the forest edge as determined on the field.*

Figure 11.2 *Shielded data-logger on the top of a 1-m high pole in forest interior.*

11.4.2 Data analysis

We computed hourly T (°C) and RH (%) as the means of the maximal and minimal values. From these hourly means, we computed the vapour deficit pressure (VPD in kPa), which is the difference between the amount of moisture in the air (VP_{air}) and how much moisture the air can hold when it is saturated {VP_{sat}, see \Arya, 2001 #478},

$$VP_{sat} = \exp^{\left(\left[(-1.88\times10^{4})/T\right]-13.1+\left[(1.5\times10^{-2})/T\right]+(8\times10^{-7}\times T^{2})+(-1.69\times10^{-11}\times T^{3})+(6.456\times\ln(T))\right.}$$

$$VP_{air} = VP_{sat} \times RH/100$$

$$VPD = VP_{sat} - VP_{air}$$

The VPD is particularly interesting to analyse and assess forest edge vulnerability to fire as it is a good proxy of litter moisture content and fire behaviour (Ray *et al.* 2010; Ray *et al.* 2005).

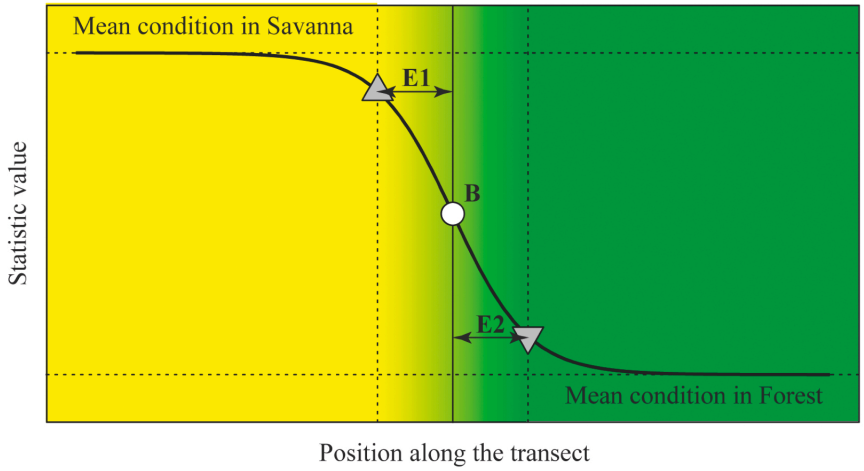


Figure 11.3 *Example of BEDA applied on the savanna-forest boundary. The mean air microclimatic conditions into savanna and forest interiors are estimates by the two asymptotes, the climatic boundary between these two habitats by the inflexion point B and the borders of the ecotone by E1 and E2. The width of the ecotone is given by E1 + E2.*

We used the border and ecotone detection analyses (BEDA) presented by Hennenberg (2008) to detect variation in microclimatic borders and ecotone between savanna and forest. BEDA is based on a sigmoidal non-linear function,

$$f(x) = a + (c - a)/(1 + \exp^{(x-b)/d})$$

where f(x) is the value of the studied statistic (T, RH or VPD), calculated as a function of the position x along the transect, a and c represent the upper and lower asymptotes (estimated mean conditions in the two adjacent habitats), b is the distance to the

inflection point (B in Figure 11.3, which is an estimation of the boundary between the two adjacent habitats) and, d characterizes the steepness of the change of the studied statistic. The limits of the ecotone (E1 and E2), which are equivalent to the depth of edge influences (DEIs) towards the two habitat interiors are given by

$$E1 = b + 2d$$

and

$$E2 = b - 2d$$

We computed BEDA on diurnal mean values (from 8 am to 4 pm) to analyse and compare the temporal variations in (i) the mean conditions in savanna and forest interiors and (ii) the limits of the ecotone and the DEIs. The parameters of the BEDA model were adjusted using non-linear least-square regression computed with the R 2.9.2 environment for statistical computing (R Development Core Team 2009). We only analysed the days for which all fitted BEDA parameters were significant ($P < 0.05$).

11.5 Results

Over the studied period, microclimatic conditions were equivalent in the three studied transects for both savanna and forest interiors conditions (Figure 11.4). Although, the T increased, the RH decreased and the VPD increased during the dry season, the amplitudes of these seasonal changes were globally low and higher in savanna for the RH and the VPD (5°C in both savanna and forest, 12 % in savanna and between 7 and 9 % in forest, and 0.6 kPa in savanna and 0.3 kPa in forest). The difference between both T and RH measured in savanna and forest was quite constant over the studied period (*ca* 5°C and 20 %, respectively) while the difference in VPD was slightly more variable (Figure 11.4). Note also that the interdaily variability in VPD was higher in savanna compared to forest.

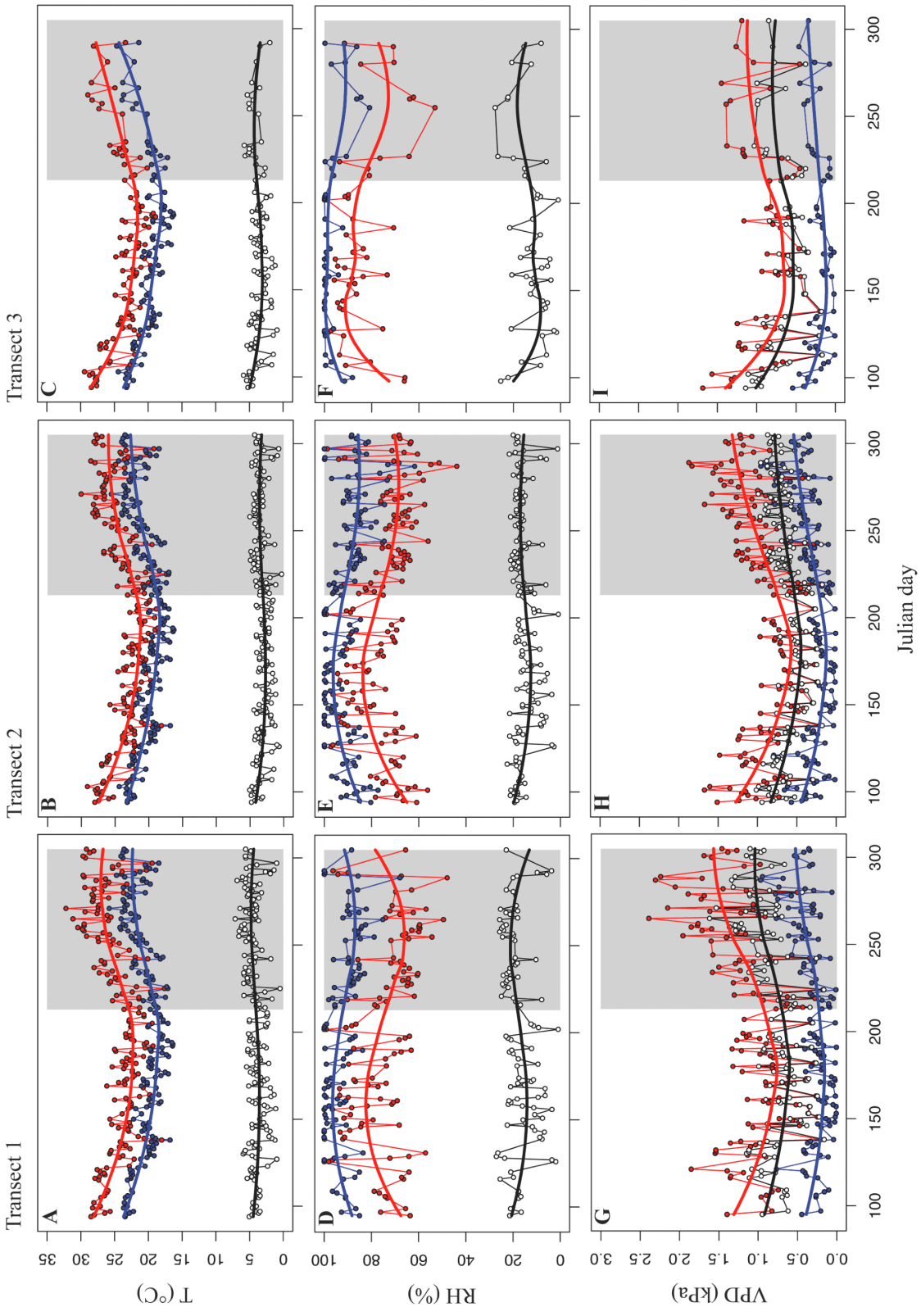
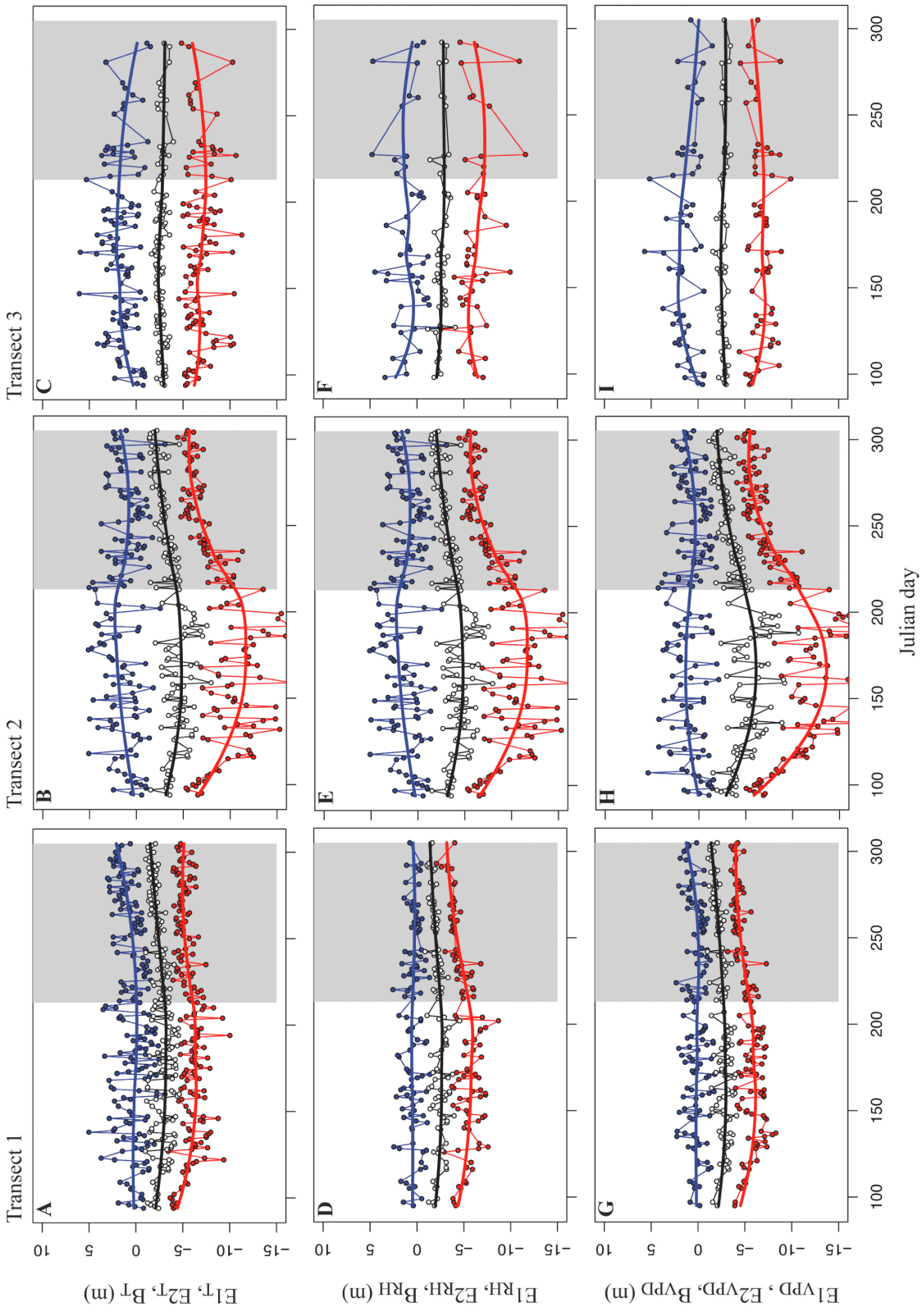

Transect 1
Transect 2
Transect 3
A
B
C
D
E
F
G
H
I
T (°C)
RH (%)
VPD (kPa)
Julian day

Figure 11.4 *(previous page) Daily mean conditions in air temperature (T), relative humidity (RH) and vapour deficit pressure (VPD) into savanna (red point) and forest (blue points) interiors estimated from BEDA along the studied period. The white points represent the differences in microclimatic mean conditions in savanna and forest. The grey area represents the expected dry season.*

Surprisingly, the positions of the ecotone borders estimated from BEDA was quite constant for the three studied microclimatic statistics, except for the savanna side ecotone border in the transect 2 (Figure 11.5 and Figure 11.6). The estimated microclimatic boundary between savanna and forest slightly shifted toward savanna (at *ca* -2.5 m) compared to the boundaries defined on the field according to vegetation structure and composition (at 0 m). The transitions of microclimatic conditions between savanna and forest were very sharp. Indeed the width of the microclimatic ecotones were approximately 5 m along the studied period except along the transect 2 during the moist season, where the width of the ecotone reached approximately 12.5 m with a shift of the boundary toward savanna (at *ca* 5 m, Figure 11.5). One of the most striking results, which invalidates our hypothesis, was that most part of the 'microclimatic' ecotone was situated outside forest. In other words, forest border was not affected by microclimatic edge effects such as drought penetration (Figure 11.6).

The profiles of the studied microclimatic conditions (T, RH and VPD) highlighted a high daily variation (Figure 11.7). The amplitude of this daily variation was more than twice higher in savanna than in forest and was slightly higher during the dry season.

Figure 11.5 *(next page) Daily position of the limits of the ecotone on the savanna side (E1, red points) and on the forest side (E2, blue points), and estimated position of the boundary between savanna and forest (B, white points) estimated from BEDA for the air temperature (T), relative humidity (RH) and vapour deficit pressure (VPD). The grey area represents the expected dry season.*


Transect 1
Transect 2
Transect 3
A
B
C
D
E
F
G
H
I
E1T, E2T, BT (m)
E1RH, E2RH, BRH (m)
E1VPD , E2VPD, BVPD (m)
Julian day

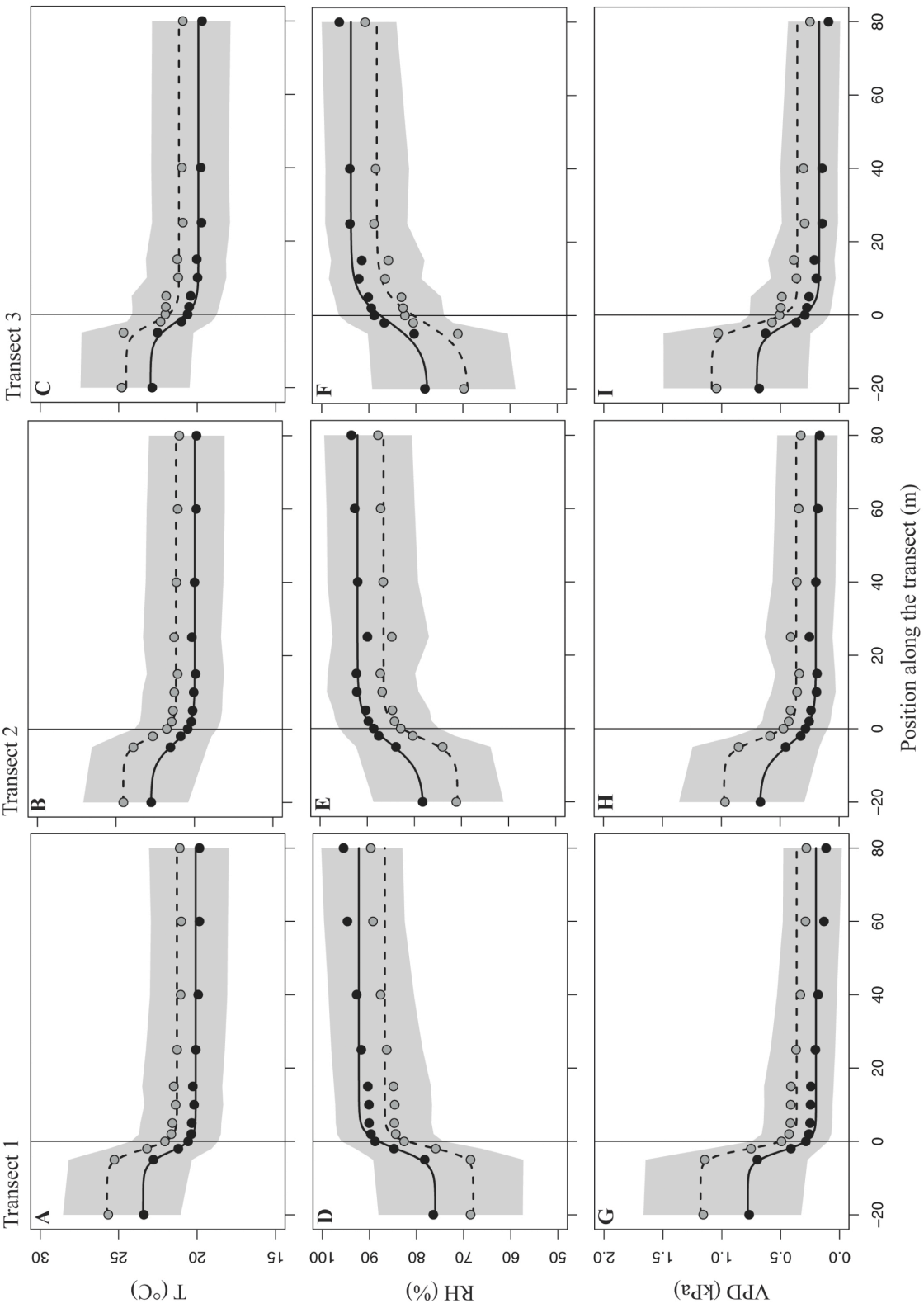

Transect 1
Transect 2
Transect 3
A
B
C
D
E
F
G
H
I
T (°C)
RH (%)
VPD (kPa)
Position along the transect (m)

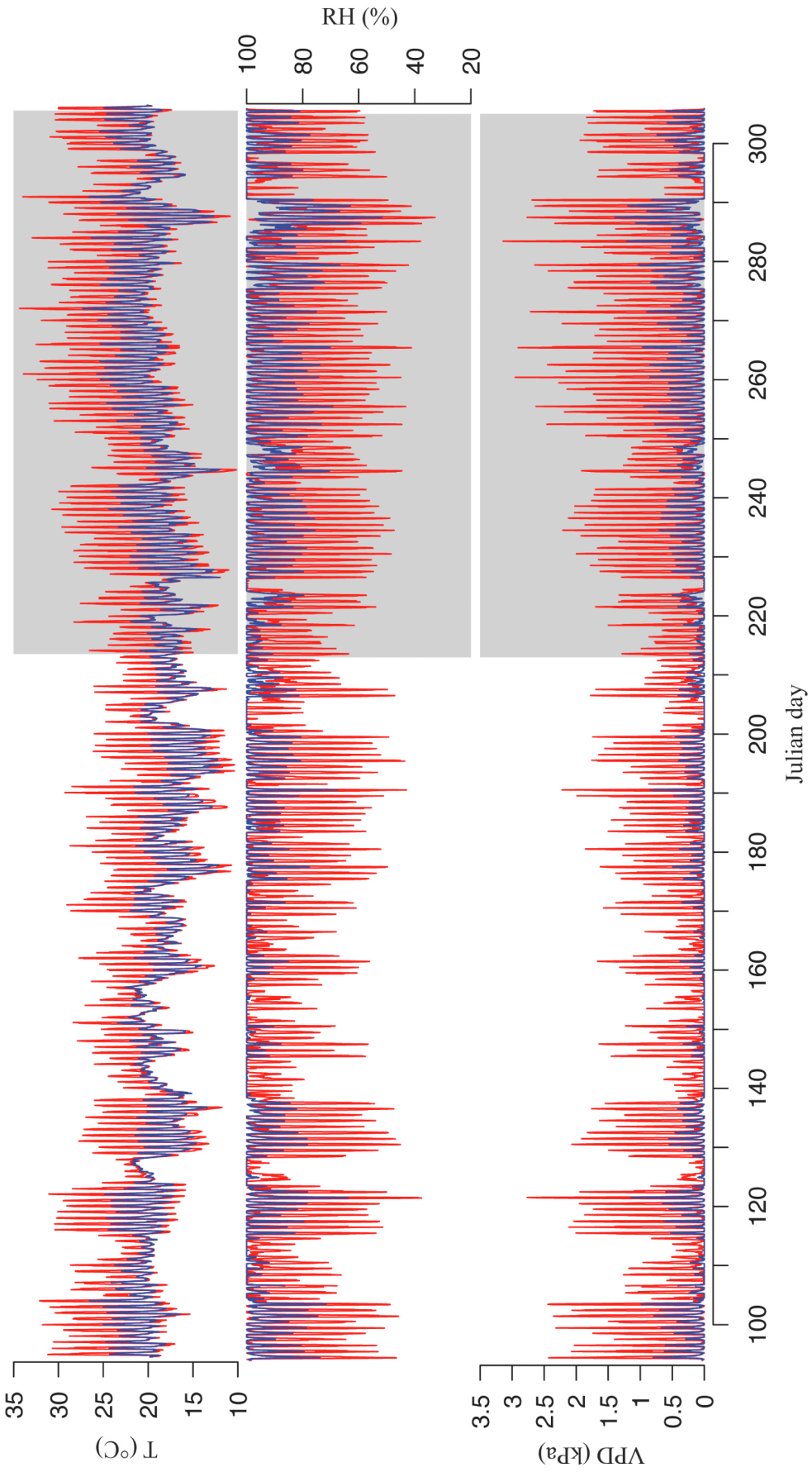
Figure 11.6 *(previous page) Mean daily air temperature (T), relative humidity (RH) and vapour deficit pressure (VPD) measure by the data loggers along the three transects during the expected humid (black points) and dry (grey points) seasons. The grey area represents on standard deviation, the full and dashed lines represent the BEDA fits. The vertical line represent the boundary between savanna and forest positioned on the field.*

Figure 11.7 *(next page) Hourly air temperature (T), relative humidity (RH) and vapour deficit pressure (VPD) along the studied period. The red and blue lines represent the averaged microclimatic condition measured by the data loggers placed at the beginning (in savanna, at -20 m) and at end (in forest, at 80 m) of the three transects, respectively. The grey area represents the expected dry season.*

11.6 Discussion

Microclimatic conditions measured along transects highlighted a sharp (*ca.* 5m) transition between savanna and rainforest all over the studied period. Such sharp transition does not impact on forest stand at it is located just outside the forest border and is characterized by moister conditions than those recorded in the savanna interior. Conversely, forested microclimatic conditions start just on the forest border and are constant along the forested transect. Such spatial pattern is found all over the studied period besides the daily and seasonal variability measured in air temperature, relative humidity and vapour deficit pressure in savanna and forest interiors.

Microclimatic conditions at the forest border and the importance of the edge effects depend on the structure of the vegetation (Didham and Lawton 1999; Matlack 1993; Ray *et al.* 2010; Ray *et al.* 2005). For instance, the studies of Matlack (1993) and Didham & Lawton (1999) showed that microclimatic edge effects such as drought penetration were greater at open edges that closed ones. Thus, as described on these two studies, the relative homogeneity of microclimatic conditions from forest border to the forest interior may be explained by the sharp transition observed in tree density as it increases in few meters from *ca* 0.1 stems.m^2 in savanna to *ca* 0.4 stems.m^2 in forest (Ibanez *et al.* in prep.-c).


RH (%)
100
80
60
40
20
T (°C)
35
30
25
20
15
10
VPD (kPa)
3.5
3
2.5
2
1.5
1
0.5
0
100
120
140
160
180
200
220
240
260
280
300
Julian day

Nevertheless, our results must be interpreted with caution. Indeed, the studied year (2010) was a relatively humid year (the rainfalls during the 2010 dry season were above the third quartile of the distribution of the rainfalls during dry season in New Caledonia), which may be partly explained by a relatively intense *la Niña* episode (R. Barbero, pers. com.). Indeed, the New Caledonian climate variability is mainly driven by the *El Niño* Southern Oscillation (ENSO) phenomenon (Ropelewski and Halpert 1987). During *El Niño* phases the rainfall decreases (down to 50 % of normals), whereas during *La Niña* phases the opposite trend is observed (Delcroix and Lenormand 1997). Thus, we can hypothesise as Hennenberg *et al.* (2008) that microclimatic ecotone between savanna and forest could likely shift to forest interior during dryer events such as *el Niño* episodes.

Our results suggest that during moist years such as *la Niña* episodes, savanna fire would not penetrate in forest understory, as it is not dried by microclimatic edge effect. This hypothesis was sustained by field observations of savanna fires, which clearly stopped at the forest edge during the studied period (pers. obs.). At global and regional scales, rainfall anomalies related to *El Niño* / *La Niña* have a strong effect on the spatiotemporal variability of fire regime (Fuller and Murphy 2006; Le Page *et al.* 2008; van der Werf *et al.* 2008a). As example, Alencar *et al*. (2004) showed in eastern Amazonia that more than 90 % of the forest area that burned between 1982 and 1999 were associated to drought induced by *el Niño*.

11.6.1 Conclusion

Contrarily to our hypothesis, the 'microclimatic' ecotone between savanna and rainforest was situated outside the forest. This result is likely due to the fact that the studied year was relatively humid (*la Niña* episode). In such conditions the vulnerability of the forest edge to savanna fires is relatively low and the moister condition in savanna close to the forest edge may promote forest expansion (Fonsca and Joner 2007). However, we suggest that during abnormally dry years (*el Niño* episodes) the savanna-forest border shift toward forest interior drying the understory and making the forest edge more vulnerable to savannas fire. Prescribed fires during humid years would limit

the fuel load accumulation in savanna without affecting the forest edge and preventing dramatic fire impacts during dry years.

11.7 Acknowledgements

We thank the ANR BDIV-07-008 project INC and the Research Federation ECCOREV (FR 3098) for funding this research, and the CNRS for funding the PhD scholarship of T. Ibanez. We are grateful to Denis Meandu-Poveu and Julien Gorodé for their help on the field.

12 Synthèse et discussion générale

12.1 Avant propos

Les forêts denses humides couvraient avant l'installation de l'Homme une grande partie de la Nouvelle-Calédonie (plus de 60 %) et ont perdu depuis de l'ordre de deux tiers de leur surface initiale (Jaffré *et al.* 1998; Jaffré and Veillon 1994). Inversement, les savanes qui n'existaient pas à l'état naturel en Nouvelle-Calédonie (Stevenson *et al.* 2001) couvrent aujourd'hui de l'ordre de 30 % du territoire (Mittermeier *et al.* 2004). A haute altitude on retrouve encore des massifs forestiers importants et relativement bien conservés alors qu'à basse et moyenne altitudes où se sont focalisés ces travaux de thèse, les forêts sont très fragmentées (Jaffré *et al.* 1998), souvent réfugiées là où les incendies ne peuvent pas les atteindre, c'est à dire dans les talwegs et le long des ruisseaux (Ibanez *et al.* submitted-b; Jaffré and Veillon 1994). A l'échelle de la Nouvelle-Calédonie, les causes ayant mené à cet état sont sans doute multiples et regroupent la conversion des espaces forestier en zone de pâturage, l'exploitation forestière, la prospection et l'exploitation minière et les incendies (Virot 1956), aujourd'hui sur les substrats volcano-sedimentaire le seul facteur affectant encore directement et à large échelle géographique les forêts denses humides semble être les incendies d'origine anthropique (aux quels il faut ajouter les activités minière sur substrats ultramafiques). Cependant leurs réels impacts et l'évolution récente des formations végétales reste très peu connue.

Aujourd'hui les principales reliques forestières se retrouvent le long de la chaine montagneuse centrale qui parcourt la Nouvelle-Calédonie dans sa longueur (culminant au nord au Mt Panié à 1628 m et au sud au Mt Humbolt à 1618 m). Ces territoires montagneux sont peu peuplés et principalement habités par des sociétés kanaks organisées en tribus. En effet, la densité de population en Province Nord qui abrite la plupart des formations forestières sur sols volcano-sedimentaires est inférieure à 5 hab.km^2, contre plus de 26 hab.km^2 en Province Sud ou se trouvent la capitale Nouméa et la plupart des massifs ultramafiques. L'analyse de la distribution spatiale des feux

détectés par les satellites MODIS et LANDSAT entre 1999 et 2010 montre que ces feux sont agrégés autours des axes routiers (longeant la côte ouest la plus peuplée et les différentes transcalédoniennes reliant la côte ouest à la côte est) et environ 10 km autour des tribus (Curt *et al.* in prep.). Bien que ce jeu de données ne reflète pas totalement l'importance de la menace que représentent les feux sur les écosystèmes néo-calédoniens, il confirme le rôle central des Hommes dans les ignitions qui conduisent à des incendies. D'autre part, cette dernière étude montre que, bien que les feux se propagent très majoritairement dans les milieux ouverts tels que les savanes, la plupart d'entre eux (64 % des feux de savanes) atteignent ou s'arrêtent à proximité des lisières forestières. Ces observations ont été confirmées par modélisation à partir de feux simulés dans le paysage de savanes et de forêts autour de Gohapin étudié dans cette thèse (Hély *et al.* in prep.).

Comme il a été détaillé en introduction, les forêts denses humides et les savanes peuvent constituer deux états stables alternatifs (Mayer and Khalyani 2011; Scheffer and Carpenter 2003; Staver *et al.* 2011b) sur une grande partie du territoire néo-calédonien. Le régime des feux, et notamment leur fréquence semble être le principale facteur déterminant le maintien de l'un de ces états, ou le passage de l'un à l'autre lorsque le régime des feux est modifié (Mayer and Khalyani 2011). Les travaux présentés dans cette thèse ont ouvert le champ portant sur les processus écologiques mis en jeu dans la dynamique et l'alternance de ces deux états en se focalisant toutefois sur le passage de la savane vers la forêt dense humide *via* la succession secondaire lorsque la fréquence des incendies diminue.

La discussion générale des résultats présentés au long de cette thèse est organisée en quatre sections. La première section discute les principaux facteurs identifiés comme dirigeant à différentes échelles spatiales et temporelles les dynamiques des forêts denses humides et des savanes à partir de la modification du régime des feux. La deuxième section discute les résultats obtenus sur la succession secondaire et synthétisera notamment l'écologie de *Geissois racemosa* qui semble être une espèce clé. La troisième section discute de la durabilité et de la résilience des écosystèmes forestiers dans ces paysages fragmentés. Enfin la quatrième section synthétise les implications de ces résultats de thèse en terme de restauration et de conservation des forêts denses humides.

12.2 Quels facteurs dirigent les dynamiques savanes - forêts denses humides en Nouvelle-Calédonie ?

Dans les paysages néo-calédoniens recevant des précipitations annuelles comprises entre 1000 et 2500 mm, les forêts denses humides et les savanes peuvent être deux états stables alternatifs (Staver *et al.* 2011b). Les dynamiques entre forêts et savanes en Nouvelle-Calédonie peuvent ainsi être comparées à une lutte (Sarlin 1954) entre ces deux états au cours de laquelle, le régime des feux est le principale arbitre (Figure 12.1). Le régime des feux de savanes, et notamment leur fréquence, déterminée par l'interaction du climat, des ignitions et de la végétation (Whelan 1995) permet le maintien ou non de ces savanes, en empêchant ou non les arbres forestiers de s'installer. Le comportement des feux quant à lui détermine si les feux se propageant dans ces savanes peuvent affecter ou non les forêts environnantes.

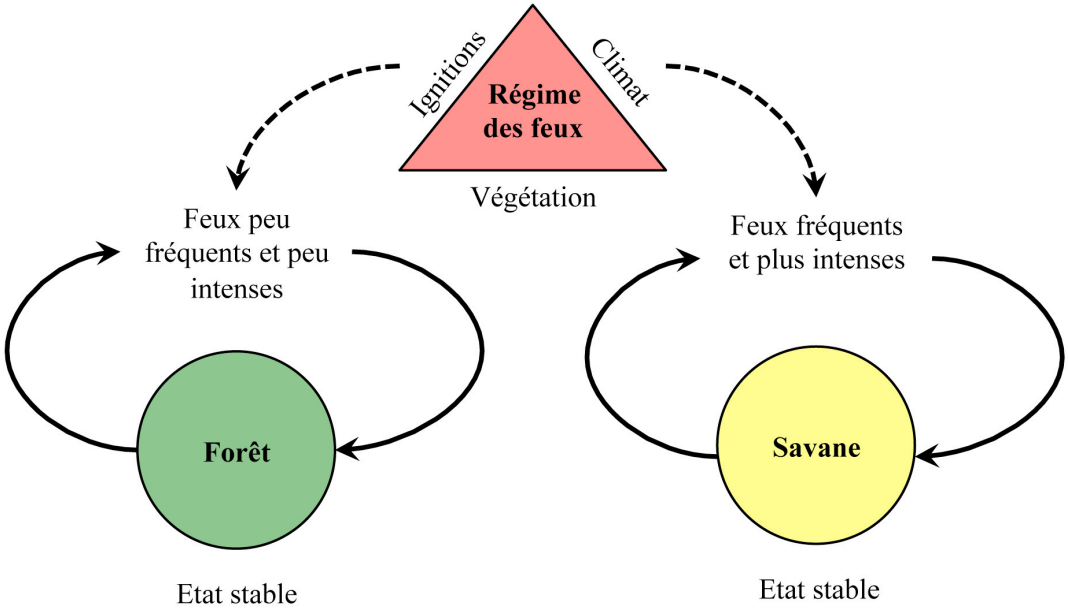


Figure 12.1 *Le régime d'incendie 'arbitre' de l'équilibre savane-forêt*

Le climat et la végétation déterminent si les conditions environnementales sont favorables ou non à la propagation des incendies. Si elles le sont, ce sont alors les ignitions qui déterminent si les feux surviennent. Le climat et les ignitions sont les variables qui semblent le plus diriger la variabilité temporelle du régime des incendies et ainsi l'équilibre entre les forêts denses humides et les savanes.

(i) Le climat

La variabilité interannuelle du climat néo-calédonien est principalement dirigée par l'oscillation austral *El Niño* (ENSO) (Delcroix and Lenormand 1997; Nicet and Delcroix 2000) qui affecte la longueur et l'intensité de la saison sèche et donc la période favorable aux incendies. Les archives météorologiques montrent ainsi une alternance de périodes normales, anormalement humides (*La Niña*) et anormalement sèches (*El Niño*). La forte influence d'ENSO sur les régimes des feux en milieu tropical est bien connue (e.g. Fuller and Murphy 2006; van der Werf *et al.* 2008b). En Nouvelle-Calédonie, sur la période 1999-2010, Curt *et al.* (in prep.) et Barbero *et al.* (in press.) ont montré que les feux étaient plus nombreux durant les évènements *El Niño*. Les périodes sèches du type *El Niño*, seraient ainsi favorables au maintien, voire à l'expansion des savanes, alors que de longues périodes humides du type *La Niña*, provoqueraient un abaissement de la fréquence des incendies et l'expansion forestière.

L'étude de la zone clé que représente la transition entre savane et forêt dense humide (sections 10 et 11), suggère que durant les périodes humides du type *La Niña,* les forêts denses humides sont peu vulnérables aux incendies se propageant dans les savanes environnantes. En effet, durant ces périodes où la saison sèche est peu marquée, des effets de bords microclimatiques offrent des conditions plus humides dans les premiers mètres de savanes bordant la forêt. Cette zone ferait alors office de 'tampon' en cas d'incendie dans la savane avoisinante et sa présence au cours de périodes humides prolongées favoriserait l'expansion forestière (Figure 12.2.A). Cette dernière hypothèse est corroborée par des observations de terrain montrant des feux de savanes s'arrêtant juste en avant de la lisière forestière (Figure 12.2.B).

A l'inverse, durant les périodes du type *El Niño*, où la saison sèche est plus intense, c'est la partie forestière qui serait soumise, *via* les effets de bords, à des conditions plus sèches (e.g. Hennenberg *et al.* 2008). Ce desséchement de la lisière forestière favoriserait alors la pénétration des feux de savanes dans le sous-bois forestier (Figure 12.2.A). Ces feux de sous-bois, liés aux effets de bords ont été fréquemment observés dans les tropiques (e.g. Cochrane and Laurance 2002). Dans l'est de l'Amazonie, Alencar *et al*. (2004) ont montré que 90 % des surfaces forestière brulées

entre 1982 et 1999, l'on été durant des périodes de sécheresse liées à *El Niño*. Les essences forestières étant peu résistante aux incendies (Hoffmann *et al.* 2003; Ibanez *et al.* submitted-a; Jackson *et al.* 1999), bien que ces feux de sous bois soient peu intenses, ils suffisent à provoquer une mortalité importante dans les peuplements forestiers (Balch *et al.* 2011; Barlow *et al.* 2003; Barlow and Peres 2008; Cochrane 2003). Cette mortalité ouvre la canopée et modifie la structure et la composition de la lisière forestière qui devient plus perméable à la sécheresse et donc plus inflammable et plus vulnérables aux incendies (Barlow and Peres 2008; Cochrane *et al.* 1999; Didham and Lawton 1999). L'accélération de la déforestation entre 1997 et 2000 sur autour de Ghoapin (section 3) pourrait être liée à l'événement *El Niño* de 1997-1998, reconnu comme étant le plus intense du 20ème siècle et qui a conduit à d'importantes pertes de forêts dues aux incendies à travers les Tropiques (Cochrane 2003; Nepstad *et al.* 1999; Siegert *et al.* 2001).

Enfin dans des conditions normales (Figure 12.2.A), les feux de savanes sont assez fréquents pour empêcher l'expansion forestière mais ils ne peuvent cependant pas pénétrer le sous-bois forestier, ce qui a pour effet d'entretenir une transition abrupte entre la savane et la forêt (Ratnam *et al.* 2011).

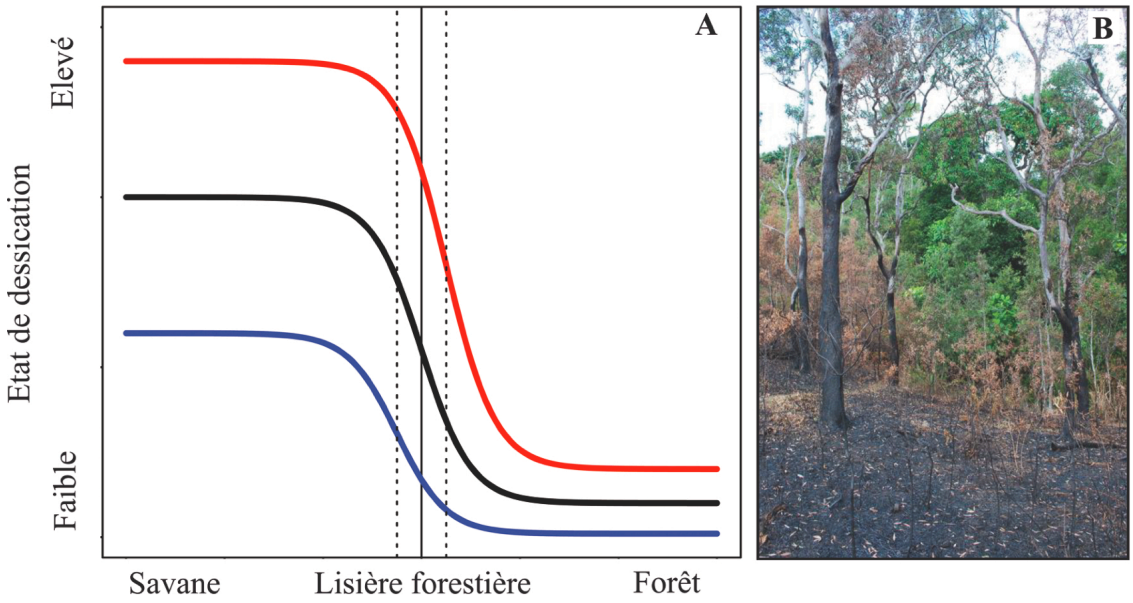


Figure 12.2 (A) *Conditions microclimatiques (état de dessiccation) le long de la zone de transition entre la savane et la forêt dense humide durant des périodes anormalement humides (type La Niña, ligne bleue), anormalement sèches (type El Niño, ligne rouge)*

et normales (ligne noire). (B) *Photographie d'un feu de savane s'étant arrêté en amont de la lisière forestière.*

Les alternances climatique liées à ENSO conduiraient donc à des phases 'instables', soit anormalement humides et favorables à l'expansion forestière (type *La Niña*), soit anormalement sèches et favorables à la contraction forestière (type *El Niño*), entrecoupées de phases 'stables' ou neutres (conditions normales). Dans le troisième chapitre de cette thèse l'analyse de la structure et de la composition de la végétation d'une zone de transition entre savane et forêt dense humide, a mis en avant le passage d'une phase 'instable' d'expansion caractérisée par une zone de recolonisation forestière, à une phase 'stable' caractérisée par une transition brutale entre cette zone et la savane (section 11). Cette dynamique pourrait être liée au passage d'une période anormalement humide à période normale, cependant elle pourrait être aussi tout simplement liée à une baisse de la pression d'ignition dans la zone.

Une modification d'ENSO liée aux changements climatiques pourrait donc avoir d'importantes implications sur les dynamiques et la distribution des forêts denses humides et des savanes. Notamment, les évènements *El Niño* pourraient s'intensifier (Li *et al.* 2007) et augmenter la vulnérabilité des forêts denses humides, cependant le future d'ENSO est encore source de débats (Christensen *et al.* 2007).

Plus largement, les changements climatiques et notamment l'évolution des précipitations peuvent modifier l'équilibre entre les savanes et les forêts denses humides. Par exemple dans le nord de l'Australie, une augmentation des précipitations associées à l'effet fertiliseur de l'augmentation du CO_2 atmosphérique serait à l'origine, malgré les feux de savanes, d'une expansion forestière (Banfai and Bowman 2007; Bowman *et al.* 2010). Toutefois, de par sa petite taille et son isolement géographique aucune projection sur le climat néo-calédonien n'existe. Nous ne pouvons donc pas faire d'hypothèses précises sur l'impact des changements climatiques sur l'équilibre entre savane et forêt denses humides en Nouvelle-Calédonie.

(ii) *Les ignitions*

Une allumette a embrasée la forêt
Je ne sais même plus si l'on peut la sauver
Tout est brulé, rasé, même carbonisé
Et tout cela c'est moi qui l'ai causé

A lire sur un air de Kaneka
Une allumette, Kass'Pa Kaneka Hyehen

Comme dans la plupart des milieux tropicaux (Stott 2000), les incendies en Nouvelle-Calédonie ont une origine anthropique. Les observations faites au cours de ces travaux de thèse (notamment au travers du co-encadrement d'un stage d'ethnoécologie, Udo 2011), et plus largement au sein du projet ANR INC dans lequel elles se sont déroulées, suggèrent que les changements socio-environnementaux qui touchent la Nouvelle-Calédonie et plus particulièrement les sociétés kanaks, provoquent une modification des usages traditionnels du feu et une apparition de nouveaux usages. Cela aurait comme conséquence directe une modification du régime des feux.

Au niveau environnemental, l'expansion des espèces invasives végétales et animales (Gargominy *et al.* 1996; Hequet *et al.* 2009) est la source principales de nouveaux usages. Le feu semble aujourd'hui être beaucoup utilisé pour nettoyer les zones envahies par des espèces tels que la Sensitive Géante (*Mimosa invisa*) ou le Lantana (*Lantana camara*) qui obstruent les déplacements en savane ou le long des sentiers de chasse. Ces 'brousses' sont aussi brulées car elles servent de refuge aux cochons sauvages (*Sus scrofa*) qui dévastent les champs fournissant des produits traditionnels de subsistance tels que l'igname ou le tarot pour ne citer que les plus importants. Ainsi, il a été observé plusieurs fois durant les missions de terrain conduites au cours de cette thèse, des versants entiers de savane brûlés à cause de cochons qui avaient dévastés des champs. Ces pratiques entretiennent un cercle vicieux car l'ouverture du milieu par les incendies semble favoriser le développement des espèces invasives (e.g. Brooks *et al.* 2004; Pauchard *et al.* 2008). Outre leurs impacts sur les

ignitions, les espèces invasives modifient la structure et la composition de la strate herbacée en savane, et au final le régime d'incendie (Brooks *et al.* 2004; Mistry and Berardi 2005). De plus, l'embroussaillement des lisières forestières par des espèces très inflammables tels que le Para (*Melinis minutiflora*) augmente leur vulnérabilité aux feux de savanes (Dobhal *et al.* 2011; Hoffmann *et al.* 2004).

Les changements socio-économiques et notamment l'occidentalisation du mode de vie kanak, sont une autre source de modification des pratiques traditionnelles (Horowitz 2001). Par exemple, la préparation des champs par brûlis semble aujourd'hui moins maitrisée qu'auparavant. Cette pratique qui s'effectuait traditionnellement à la fin de la saison humide se prolonge aujourd'hui durant la saison sèche et conduit à des feux non maitrisés qui se propagent en savane. Il semblerait aussi que des espèces invasives très inflammables tel que le Para (*Melinis minutiflora*) rendent encore plus difficile la maîtrise de ces feux.

Ainsi, la diminution globale du couvert forestier entre 1955 et 2000 autour de la tribu de Gohapin (section 3), pourrait être en partie due à une augmentation des ignitions liées à ces nouveaux usages. Inversement, il semblerait que dans une autre tribu voisine (Pöö), également située autour du massif de L'Aoupinié, l'abandon des usages du feu conduit à une fermeture progressive des savanes (Udo 2011). De la même manière, l'expansion forestière mise en avant dans le troisième chapitre de cette thèse (section 10) pourrait donc être due à un abandon temporaire de l'usage du feu dans le voisinage.

L'Homme en tant que déclencheur des incendies tient une place centrale au cœur de ce socio-éco-système. Les modifications d'usages des feux liées aux changements socio-environnementaux ont un impacte critique sur l'équilibre entre savanes et forêts. Comme suggéré par Wright et Muller-Landau (2006a) à l'échelle globale, les changements démographiques tel que l'exode rural, pourraient conduire à une expansion forestière. En Nouvelle-Calédonie, l'occidentalisation du mode vie kanak semble d'hors et déjà conduire à une migration des jeunes des populations rurales où tribales vers les zones urbaines, principalement Nouméa (voir le site de l'Institut de la Statistique et des Etudes Economiques, http://www.isee.nc/). A long terme, ces migrations pourraient ainsi faire baisser les ignitions dans les zones les plus reculées de la Nouvelle-Calédonie et favoriser l'expansion forestière.

(iii) *Topographie et structure du paysage*

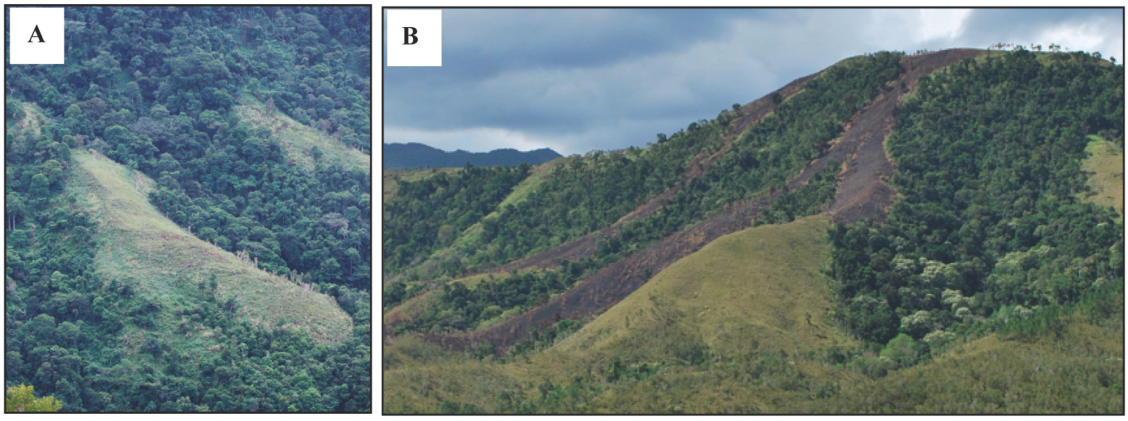


Figure 12.3 *Photographies illustrant l'impact de la topographie sur la distribution des savanes et des forêts dans les paysages soumis aux incendies. (A) Savane sur crête dans massif forestier et (B) forêts de talwegs.*

Contrairement au climat, à la pression d'ignition et à la végétation, la topographie est le seul facteur affectant le régime des feux que l'on puisse considérer comme temporellement statique à l'échelle de la dynamique des écosystèmes étudiés. La topographie, très variable le long de la chaîne centrale de Nouvelle-Calédonie, structure ainsi fortement la distribution des forêts et des savanes. En effet, il a depuis longtemps été observé (Figure 12.3) que les versants et les crêtes exposés aux vents dominants étaient favorables à la propagation des incendies et à l'installation de savane, alors que à l'inverse les talwegs et les bords de ruisseaux, plus humides, constituaient des refuges forestiers (Aubréville 1965; Jaffré *et al.* 1997b; Virot 1956). Le premier chapitre de cette thèse (section 3), a fournit à partir de l'étude d'une série diachronique de photographies aériennes, une analyse plus fine de l'importance de la topographie dans la distribution et la dynamique des forêts et des savanes à l'échelle du paysage. Outre confirmer et préciser les observations faites par ces précédents auteurs, ce chapitre suggère que la dégradation des paysages forestiers néo-calédoniens de moyenne altitude pourrait conduire à un état d'équilibre où les forêts ne subsisteraient que dans les refuges que sont les talwegs et les abords des ruisseaux. Ces travaux ont été complétés par Hély et al. (in prep.) qui ont analysé par modélisation la propagation des incendies au sein du même paysage. Ils ont notamment montré que la propagation des incendies

de savanes était en fait systématiquement stoppée par l'association d'un passage de crête, qui freine la propagation, et d'une lisière forestière située en contre bas, qui fournit un combustible moins inflammable.

La distribution spatiale des forêts et des savanes, bien que fortement liée à la topographie, dépend avant tout de l'utilisation des terres par les Hommes. En effet, même si une zone est topographiquement favorable à l'installation de savane *via* la propagation d'incendies, s'il n'y a pas d'ignition, les feux n'auront pas lieux et la forêt sera maintenue en place. Cela a été bien mis en avant dans le premier chapitre de cette thèse par la présence d'un important fragment forestier sur une zone topographiquement favorable à la propagation des incendies. Il s'est avéré que cette forêt était protégée par son statut de 'zone Tabou' (i.e. forêt sacrée) qui interdisait l'utilisation du feu dans son voisinage (Figure 12.4).

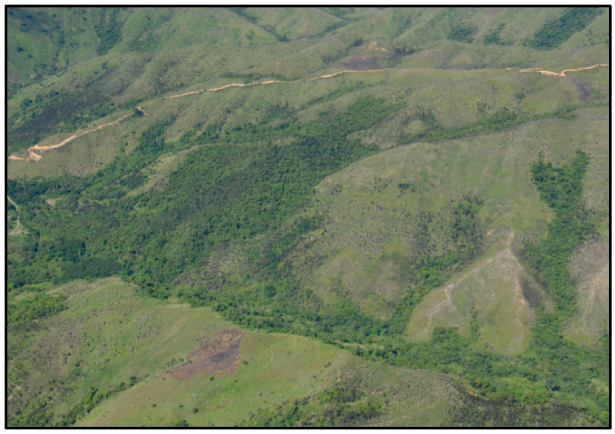


Figure 12.4 *Photographie montrant la fragmentation des forêts par les feux et l'influence de l'utilisation des terres, avec en partant de la droite vers la gauche deux forêts de talwegs très réduites puis une forêt beaucoup plus importante vraisemblablement grâce à son statut 'Tabou' ou sacré.*

12.3 Succession secondaire

12.3.1 Blocage de la succession et maintien des savanes

Dans les zones où le pâturage est absent comme c'est le cas sur une grande partie de la Nouvelle-Calédonie (mise à part le long de la cote ouest) les incendies semblent être le principal facteur maintenant les savanes en bloquant la succession secondaire. En effet, les espèces pionnières, pouvant pousser dans les conditions difficiles de la savane (sécheresse, fort ensoleillement, compétition avec la strate herbacée) sont cependant peu tolérantes aux incendies qui s'y propagent (section 6), alors que les populations de Niaoulis (*Melaleuca quinquenervia*) qui dominent les savanes, non seulement tolèrent ces incendies, mais sont aussi dans une certaine mesure favorisés dans leurs développements par ces derniers (section 7). Ainsi, bien que ces résultats souffrent d'un manque de donnée sur la vitesse de croissance de ces espèces, un intervalle de temps important entre deux feux semble nécessaire pour qu'elles puissent s'installer et atteindre la taille leurs permettant de résister aux incendies par une épaisseur d'écorce suffisante et une hauteur de base du houppier au dessus des flammes. Parmi les espèces étudiées, *Geissois racemosa*, *Codia albicans* et *Tabernaemontana cerifera* semblent toutefois être plus tolérantes que les autres et pourraient s'installer durablement en savane plus facilement que les autres. La succession secondaire ne semble donc pouvoir se mettre réellement en place que lorsque il y a un abandon local des pratiques d'usage des incendies. En effet, la plupart des formations secondaires étudiées (section 4) étaient situées dans des zones où l'usage du feu avait été était abandonné (e.g. zone de protection du WWF, zone abandonnée ou volonté des propriétaires de limiter l'usage du feu).

En l'absence d'incendie, la mise en place d'une succession secondaire nécessite l'apport de graines d'espèces capables de pousser en savane. Cette limite a été mise en avant dans le premier chapitre de cette thèse (section 3), qui démontre que même lorsque les conditions topographiques sont favorables à l'installation d'une succession secondaire (i.e. protègées des incendies), celle-ci est limitée par la quantité et la proximité des sources de graines. Ce résultat a été corroboré par le faible apport de graines mesuré dans une zone où les formations forestières avoisinantes étaient rares et

fragmentées (section 8). La plupart des espèces de début de succession identifiées au long de cette thèse et plus largement les espèces forestières néo-calédoniennes (Carpenter *et al.* 2003; Gailhbaud 2009) sont dispersées par les oiseaux. La dispersion par les agents biologiques tels que les oiseaux est fortement influencée par la structure et la composition du paysage (Herrera and Garcia 2010; Levey *et al.* 2005; McDonnell and Stiles 1983). Il a été montré que la présence de perchoirs naturels ou artificiels permettait d'augmenter l'attractivité d'un site pour les oiseaux et au final l'apport de graines (e.g. Holl 1998; Holl *et al.* 2000; Slocum and Horvitz 2000). En Nouvelle-Calédonie, l'installation d'arbres tels que *Geissois racemosa* en savane, semble avoir un effet positif sur l'apport de graines *via* un tel effet perchoir (section 8).

La compétition avec la strate herbacée constitue l'une des autres principales barrières à l'installation d'espèces forestières en savane (Bond 2008; Hooper *et al.* 2005; Zimmerman *et al.* 2000). Bien que cette partie n'ait pas été développée au long de cette thèse, les observations de terrain sur la prolifération des espèces invasives et les résultats préliminaires sur l'impact du Lantana (*Lantana camara)* sur cette installation (section 9) suggèrent que ces espèces invasives jouent un rôle critique dans le ralentissement ou l'empêchement de la succession secondaire.

Enfin il faut noter que la répétition des feux mettant les sols à nu, suivis de forts évènements de précipitations qui entrainent une érosion et un appauvrissement des sols, sont aussi susceptibles de ralentir ou d'empêcher la mise en place d'une succession secondaire. Ces processus sont encore plus importants sur les zones de crêtes où l'érosion est plus forte et où très peu de sol subsiste. De plus le Niaouli (*Melaleuca quinquenervia*) qui a la caractéristique de dessécher les sols (Virot 1956) peut rendre l'installation des espèces forestières plus difficile. Pour finir, bien que le pâturage lié à l'élevage extensif soit absent, la prédation par le Cerf rusa (*Cervus timorensis russa*), dont les populations sont très développées en Nouvelle-Calédonie peut aussi limiter le succès d'installation des arbres en savane (De Garine-Wichatitsky *et al.* 2005).

12.3.2 Modèle et processus succession secondaire

Malgré les barrières énoncées dans la section précédente, des successions secondaires arrivent à se mettre en place. Sarlin (1954) avait déjà observé des Niaoulis (*Melaleuca*

quinquenervia) en lisière forestière dont il attribuait la présence à une installation dans la forêt. Ces travaux de thèse démontrent au contraire que la présence de Niaoulis dans des formations forestières indique une fermeture de la savane par succession secondaire (section 3, 4 et 10). Ces populations de Niaoulis, intolérant à l'ombrage et incapables de se régénérer dans le sous-bois, disparaissent peu à peu au cours de la succession (section 4 et 10).

Les successions secondaires de la savane vers la forêt dense humide ne sont à notre connaissance que très peu documentées en Nouvelle-Calédonie. Durant ces travaux de thèse, une combinaison originale de données de terrain et de données d'herbiers, a permis de définir une liste des principales espèces pionnières et d'identifier deux modèles de successions secondaires (section 4).

Figure 12.5 *Formations à Codia albicans, (A) bourrelet cicatriciel (formation à Codia albicans entourée par une ligne pointillée) et (B) fermeture d'une crête.*

Le premier modèle correspond à des formations mono-dominantes, dominées par une espèce anémochore, *Codia albicans,* qui semble conduire à une rapide fermeture de la canopée mais à un lent retour de la diversité d'arbres (voir section 4). L'analyse des données d'herbier, et les observations de terrain montrent que différentes formations à *Codia* spp. existent en Nouvelle-Calédonie. Ces formations forment souvent des 'bourrelets cicatriciels' le long des lisières forestières (Figure 12.5.A) ou referment les savanes sur crêtes (Figure 12.5.B). Toutefois l'origine et le devenir de ces formations qui peuvent s'apparentées aux formations à *Nothophagus* spp. sur substrats ultramafiques (Read *et al.* 1995; Read *et al.* 2006) restent floues.

Le deuxième modèle de succession secondaire correspond à des formations mixtes, co-dominées par des espèces anémochores (*e.g. Geissois racemosa* et *Alstonia costata*) et ornithochores (*e.g. Guioa villosa* et *Pittosporum simsonii*) qui semble conduire à une fermeture de la canopée plus lente mais associée à un retour plus rapide de la diversité d'arbres (sections 4 et 5). Contrairement aux formations à *Codia albicans*, il semble certain que ce type de formation secondaire évolue graduellement vers des formations forestières plus riches et plus complexes (section 10).

12.3.3 *Geissois racemosa* une espèce clé de la dynamique savane-forêt ?

Le Faux-Tamanoux (*Geissois racemosa*) est une espèce particulièrement intéressante qui pourrait se révéler être une espèce clé dans les dynamiques forêt-savane. En effet cette espèce qui présente une longue durée de vie se retrouve à la fois isolée en savane et dominante dans les formations forestières (notamment les formations de talweg, (Figure 12.6). Alors qu'elle semble incapable de se régénérer en sous-bois (section 4), des individus de plus de 70 cm de diamètre à hauteur de poitrine, situés en forêt à plus de 40 m de la lisière forestière ont même étaient inventoriés (section 10).

Geissois racemosa est une espèce anémochore et héliophile qui semble s'établir facilement en savane (section 4). Elle est d'ailleurs utilisée avec succès dans les programmes de restauration forestière du WWF. De plus parmi les espèces pionnières étudiées c'est celle qui présente la tolérance aux incendies la plus élevée. En effet, au stade juvénile *Geissois racemosa* est déjà capable de rejeter (Figure 12.6.B), les individus ont une croissance en hauteur rapide et ils produisent rapidement une écorce

épaisse qui leur permet de résister aux incendies (section 6). Ainsi il n'est pas rare de trouver des individus isolés en savane ou peu d'arbres mis à part des Niaoulis subsistent. Des cicatrices de feux portées par ces individus témoignent de leurs résistances aux incendies (Figure 12.6.D). Ils pourraient jouer un rôle clé dans la succession secondaire en favorisant les processus de recolonisation par nucléation (Reis *et al.* 2010; Schlawin and Zahawi 2008) en favorisant localement l'apport de graines. En effet *Geissois racemosa* se distingue du Niaouli par sa plus grande taille et sa canopée plus dense et semble ainsi être un perchoir plus attractif pour les disperseurs (section 8). Contrairement au *Codia spp.* qui forme des populations denses, les populations de *Geissois racemosa* sont plus diffuses (section 5), ce qui pourrait s'expliquer par une dispersion plus efficace en terme de distance (section 4). Ainsi les grands semenciers qui dominent les forêts de talwegs pourraient être d'importantes sources de graines pour la recolonisation des savanes environnantes.

Enfin il faut noter que *Geissois racemosa* fourni un bon bois d'œuvre (Sarlin 1954; Sebert 1874) et est une espèce mellifère qui peut favoriser la production miel, activité en développement dans la tribu de Gohapin autour de laquelle ont eu lieu ces travaux de thèse.

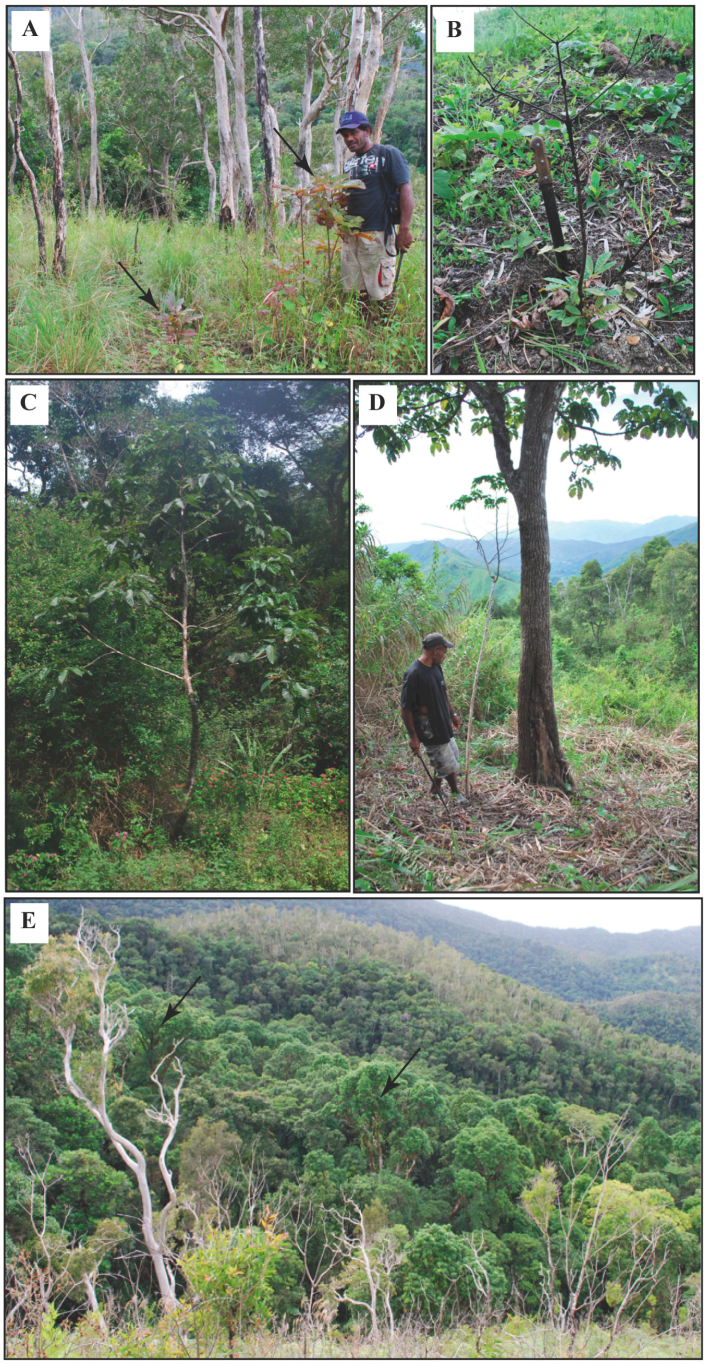


Figure 12.6 *Photographies de Geissois racemosa, (A) jeunes pousses de G. racemosa en savane, (B) jeune pousse de G. racemosa rejetant après le passage d'un feu, (C) G. racemosa en lisière forestière, (D) G. racemosa isolé en savane présentant une cicatrice laissé par les feux (E) G. racemosa dominant une forêt de talweg.*

12.4 Résilience des écosystèmes forestiers dans les mosaïques savane - forêt denses humides.

"*Building and maintaining resilience of desired ecosystem states is likely be the most pragmatic and effective way to manage ecosystems in the face of increasing environmental change."*

Scheffer *et al.* 2001

(Nature)

La résilience d'un système se caractérisant par des états alternatifs stables (ASS) tels que les savanes et les forêts denses humides en Nouvelle-Calédonie, est étroitement liée aux perturbations que ce système peut absorber avant de basculer vers un nouvel état ou un nouveau système (Gunderson 2000). La résilience des écosystèmes forestiers en terme de structure et de composition taxonomique est fortement liée la diversité taxonomique (diversité α) et plus particulièrement à la diversité fonctionnelle des espèces qu'il abrite, mais aussi à la diversité des écosystèmes à l'échelle du paysage (diversité β) qui définit un pool d'espèces régional (Thompson *et al.* 2009). Le changement d'état de la forêt dense humide vers la savane peut être facilité si la résilience de la forêt est diminuée par l'action de l'Homme *via* (i) la disparition de certains groupes fonctionnels d'espèces (e.g. disperseurs ou espèces végétales pionnières), (ii) les changements environnementaux (e.g. introduction d'espèces invasives nuisibles) ou encore (iii) la modification du régime de perturbations tels que les incendies (Folke *et al.* 2004; Gunderson 2000). L'impact des changements environnementaux et de la modification du régime des incendies ont déjà été discutés dans les sections précédentes.

La fragmentation des écosystèmes forestiers augmente l'importance des effets de bords comprenant des effets abiotiques (i.e. modification des conditions environnementales tel que le microclimat), biotiques directs (i.e. changement dans l'abondance et la distribution des espèces) et indirects (i.e. modification des interactions entre les espèces tels que la compétition et la dispersion) (Murcia 1995). Par exemple, la fragmentation et l'isolement des fragments forestiers modifient les interactions entre les espèces et notamment la dispersion des graines par les oiseaux à travers le paysage

(Herrera and Garcia 2010) et particulièrement celle des grosses graines (Cramer *et al.* 2007). La grande majorité des espèces forestières étant dispersée par les oiseaux (ou les chauves-souris) en Nouvelle-Calédonie (Carpenter *et al.* 2003; Gailhbaud 2009), la fragmentation des forêts a certainement un fort impact sur les flux de graines. Par exemple, Carpenter *el al.* (2003) suggèrent que le Notou (*Ducula goliath*, le plus gros pigeon arboricole du monde), endémique et emblématique de la Nouvelle-Calédonie, est le seul à pouvoir disperser les graines des fruits ayant un diamètre supérieur à 2 cm. Hors ce pigeon est strictement forestier et ne semble se déplacer que dans les zones forestières relativement bien préservées. Ainsi la fragmentation et l'isolement des peuplements forestiers empêchant son déplacement limiteraient la dispersion de nombreuses essences forestières (Carpenter *et al.* 2003; Gailhbaud 2009).

La fragmentation progressive des écosystèmes forestiers par la répétition des incendies mène à un appauvrissement de la diversité biologique et fonctionnelle des fragments forestiers (e.g. Abadie *et al.* 2011). Dans le paysage étudié, la fragmentation progressive des forêts denses humides semble conduire à un état stable ou les forêts ne persistent que dans les endroits inaccessibles aux feux, i.e. dans les talwegs et le long des ruisseaux (Section 3). Toutefois, la structure, la composition ainsi que la durabilité et la capacité de ces formations forestières à s'étendre dans les savanes avoisinantes restent très peu connues. Les conditions particulières de ces refuges forestiers pourraient conduire à une homogénéisation fonctionnelle des espèces présentes, et la fragmentation doit certainement limiter l'apport de graines de nouvelles espèces provenant d'autres fragments forestiers. Ces fragments forestiers pourraient alors perdre leur capacité d'expansion sur les savanes environnantes.

La restauration de l'état désiré tel que la forêt dense humide à partir d'un autre état tel que la savane demande des actions importantes et coûteuses (e.g. reforestation active). Les études récentes autour des systèmes supportant des ASS suggèrent que les stratégies pour la gestion d'un écosystème exposé à des changements environnementaux tels que les forêts néo-calédoniennes, doivent se concentrer sur le maintien de leurs résiliences (Folke *et al.* 2004; Gunderson 2000; Scheffer and Carpenter 2003).

Il semble ainsi crucial de mieux connaitre l'impact de la fragmentation sur la composition, la structure et le fonctionnement des écosystèmes forestiers afin d'essayer de maintenir ou de restaurer un degré de fragmentation leur assurant une résilience

suffisante. La restauration de cette résilience pourrait passer par la reconstruction de corridors écologiques importants entre les fragments forestiers.

12.4.1 Six points pour la gestion et la conservation écosystèmes forestiers soumis aux incendies dans les paysages fragmentés de Nouvelle-Calédonie.

" *The successful restoration of a distrubed ecosystem is the acid test of our understanding of that ecosystem."*

Bradshaw

Restoration :an acid test for ecology (1987)

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[1] La succession secondaire permettant une expansion naturelle de la forêt sur la savane ne semble pouvoir se mettre en place que lorsque les incendies sont exclus durant une longue période (de l'ordre de décennie).

[2] Dans les zones où la fragmentation de la forêt est élevée, l'apport naturel de graines semble faible et limitant pour la succession secondaire. Celui-ci pourrait être augmenté par effet perchoir en enrichissant les savanes d'arbres ou d'îlots d'arbres ayant une forte attractivité pour les disperseurs. Un apport artificiel de plants semble toutefois incontournable dans les zones les plus dégradées.

[3] Ces travaux de thèse fournissent une liste d'espèces poussant naturellement en savane et pouvant être utilisées dans des projets de restaurations forestières. Les espèces de la famille des *Cunoniaceae* et notamment le Faux Tamanou (*Geissois racemosa*) semblent particulièrement intéressantes de par leur capacité à pousser dans des zones fortement dégradées et leur tolérance aux incendies.

[4] L'exposition aux incendies et la distribution des savanes et des forêts est fortement structurée par la topographie. La restauration de zones protégées des incendies, tels que les talwegs où les bords de ruisseaux pourrait être un bon moyen de limiter la fragmentation des écosystèmes forestier en recréant de la connectivité entre les peuplements forestiers.

[5] L'utilisation du feux comme moyen de lutte contre les espèces invasives végétales et animales, bien que contre-productif, semble être l'une des principales sources d'incendies affectant les écosystèmes forestiers. Les espèces invasives végétales ont certainement un impact multiple en modifiant le régime d'incendies et en freinant ou stoppant par compétition la succession secondaire.

[6] Une gestion active des feux pourrait limiter leurs impacts sur les fragments forestiers restants en prescrivant des feux peu sévères durant les périodes humides (*La Niña*, ou avant la saison sèche) pour empêcher l'occurrence de feux beaucoup plus sévères durant les périodes sèches (*El Niño,* ou saison sèche). Une telle gestion est notamment développée dans les territoires du nord de l'Australie (Parr and Andersen 2006; Williams *et al.* 1999; Williams *et al.* 1998).

12.4.2 Conclusion

Ces travaux de thèse ont ouvert un champ de recherche critique pour la gestion et la conservation des forêts denses humides en Nouvelle-Calédonie. Ils fournissent des premiers résultats et des pistes de recherches qui doivent être complétés dans l'avenir afin d'acquérir les connaissances nécessaires à une gestion durable des forêts calédoniennes face aux incendies.

Les incendies en Nouvelle-Calédonie ont de multiples enjeux incluant la protection de la biodiversité et celle de nombreux services écosystémiques liés aux forêts. Parmi ces services écosystèmiques le maintien des sols, la régulation de l'écoulement des eaux pluviales et la fourniture en eau potable sont critiques pour le bien être des populations locales mais ont aussi des enjeux dans la conservation du lagon classé au patrimoine mondiale de l'humanité.

En vue d'une implication plus grande de la Nouvelle-Calédonie dans la lutte contre les changements climatiques *via* la réduction des gaz à effet de serre, l'étude des dynamiques forestières prend encore plus d'importance. En effet la Nouvelle-Calédonie, dont l'économie repose principalement sur l'exploitation du nickel, est un grand émetteur de gaz à effet de serre (parmi les plus gros émetteurs ramené à la population avec au total 7 Mt de CO2 par an prévus en 2012). Ainsi, la réduction des

incendies et la restauration des forêts offrent un fort potentiel de séquestration du carbone pour compenser les émissions.

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15 Références

Abadie J.-C., Machon N., Muratet A. & Porcher E. (2011) Landscape disturbance causes small-scale functional homogenization, but limited taxonomic homogenization, in plant communities *J. Ecol.* **99**, 1134-42.

Aide T. M. & Cavelier J. (1994) Barriers to lowland tropical forest restoration in the Sierra Nevada de Santa Marta, Colombia. *Restoration Ecology* **2**, 219-29.

Alencar A. A. C., Solorzano L. A. & Nepstad D. C. (2004) Modeling forest understory fires in an eastern Amazonian landscape. *Ecol. Appl.* **14**, S139-S49.

Alexander M. E. (1982) Calculating and interpreting forest fire intensities. *Can. J. Bot.-Rev. Can. Bot.* **60**, 349-57.

Andrews P. L., Bevins C. D. & Seli R. C. (2008) BehavePlus fire modeling system, version 4.0: User's Guide. United States Departement of Agriculture, Forest Service, Rocky Mountain Research Station.

Archibald S. & Bond W. J. (2003) Growing tall vs growing wide: tree architecture and allometry of *Acacia karroo* in forest, savanna, and arid environments. *Oikos* **102**, 3-14.

Arteaga L. L., Aguirre L. F. & Moya M. I. (2006) Seed rain produced by bats and birds in forest islands in a neotropical savanna. *Biotropica* **38**, 718-24.

Arya P. S. P. (2001) *Introduction to micrometeorology. 2nd edition.* Academic Press, San Diego.

Aubréville A. (1965) Instabilité de l'équilibre biologique des forêts de l'Australie orientale et de la Nouvelle-Calédonie. *Comptes Rendus de l'Academie Des Sciences* **261**.

Aubréville A., Leroy J.-F., MacKee H. S. & Morat P. (1967-present) *Flore de la Nouvelle-Calédonie et Dépendances*. Muséum National d'Histoire Naturelle, Paris.

Baddeley A. & Turner R. (2005) spatstat: An R Package for Analysing Spatial Point Patterns. *Journal of Statistical Software* **12**.

Balch J. K., Nepstad D. C., Brando P. M., Curran L. M., Portela O., de Carvalho O. & Lefebvre P. (2008) Negative fire feedback in a transitional forest of southeastern Amazonia. *Glob. Change Biol.* **14**, 2276-87.

Balch J. K., Nestpad D. C., Curran L. M., Brando P. M., Portela O., Guilherme P., Reunin-Scherer J. D. & de Carvalho Jr. O. (2011) Size, species, and fire

behavior predict tree and liana mortality from experimental burns in the Brazilian Amazon. *For. Ecol. Manage.* **261**, 68-77.

Balfour D. A. & Midgley J. J. (2006) Fire induced stem death in an African acacia is not caused by canopy scorching. *Austral Ecology* **31**, 892-6.

Banfai D. S. & Bowman D. (2008) Landscape-Scale Factors Influencing Forest Dynamics in Northern Australia. In: *Patterns and Processes in Forest Landscapes: Multiple Use and Sustainable Management* (eds R. Lafortezza, J. Chen, G. Sanesi and T. R. Crow) pp. 107-24. Springer, Netherlands.

Banfai D. S. & Bowman D. M. (2006) Forty years of lowland monsoon rainforest expansion in Kakadu National Park, Northern Australia. *Biological Conservation* **131**, 553-65.

Banfai D. S. & Bowman D. M. J. S. (2007) Drivers of rain-forest boundary dynamics in Kakadu National Park, northern Australia: a field assessment. *Journal of Tropical Ecology* **23**, 73-86.

Barbero R., Moron V., Mangeas M. & Despinoy M. (in press.) relationships between MODIS and ATSR fires and atmospheric variability in New Caledonia. *Journal of Geophysical Research*.

Barlow J., Lagan B. O. & Peres C. A. (2003) Morphological correlates of fire-induced tree mortality in a central Amazonian forest.

Barlow J. & Peres C. A. (2008) Fire-mediated dieback and compositional cascade in an Amazonian forest. *Philosophical Transactions of the Royal Society B-Biological Sciences* **363**, 1787-94.

Barnosky A. D., Matzke N., Tomiya S., Wogan G. O. U., Swartz B., Quental T. B., Marshall C., McGuire J. L., Lindsey E. L., Maguire K. C., Mersey B. & Ferrer E. A. (2011) Has the Earth's sixth mass extinction already arrived? *Nature* **471**, 51-7.

Bauer G., Speck T., Blomer J., Bertling J. & Speck O. (2010) Insulation capability of the bark of trees with different fire adaptation. *Journal of Materials Science* **45**, 5950-9.

Beerling D. J. & Osborne C. P. (2006) The origin of the savanna biome. *Glob. Change Biol.* **12**, 2023-31.

Besag J. E. (1977) Comments on Ripley's paper. *J. Roy. Stat. Soc.* **B 39**, 193-5.

Biddulph J. & Kellman M. (1998) Fuels and fire at savanna-gallery forest bounadaries in southeastern Venezuela. *Journal of Tropical Ecology* **14**, 445-61.

Bivand R., Muller W. G. & Reder M. (2009) Power calculations for global and local Moran's I. *Computational Statistics & Data Analysis* **53**, 2859-72.

Bocquet A., Chambrey C., Derroire G. & Tassin J. (2007) Modalities of colonization of woody savannah by dry forest plants in New Caledonia. *Revue D'Ecologie-La Terre Et La Vie* **62**, 87-91.

Boiteau P. (1981) Apocynacées. In: *Flore de la Nouvelle-Calédonie et Dépendances* (eds A. Aubréville and J.-F. Leroy) pp. 1-302. Muséum National d'Histoire Naturelle, Paris.

Bond W. J. (2008) What Limits Trees in C-4 Grasslands and Savannas? *Annu. Rev. Ecol. Evol. Syst.* **39**, 641-59.

Bond W. J. & Keeley J. E. (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends Ecol. Evol.* **20**, 387-94.

Bond W. J. & Midgley J. J. (2001) Ecology of sprouting in woody plants: the persistence niche. *Trends Ecol. Evol.* **16**, 45-51.

Bossdorf O., Schurr F. & Schumacher J. (2000) Spatial patterns of plant association in grazed and ungrazed shrublands in the semi-arid Karoo, South Africa. *Journal of Vegetation Science* **11**, 253-8.

Bouchet P., Jaffré T. & Veillon J. M. (1995) Plant extniction in New Caledonia - protection of scleropyll forests urgentlty needed. *Biodiversity and Conservation* **4**, 415-28.

Boughton E. A., Quintana-Ascencio P. F., Menges E. S. & Boughton R. K. (2006) Association of ecotones with relative elevation and fire in an upland Florida landscape. *Journal of Vegetation Science* **17**, 361-8.

Bova A. S. & Dickinson M. B. (2005) Linking surface-fire behavior, stem heating, and tissue necrosis. *Can. J. For. Res.-Rev. Can. Rech. For.* **35**, 814-22.

Bowman D. M. J. S., Murphy B. P. & Banfai D. S. (2010) Has global environmental change caused monsoon rainforests to expand in the Australian monsoon tropics? *Lanscape Ecology* **25**, 1247-60.

Bradford J. & Jaffre T. (2004) Plant species microendemism and conservation of montane maquis in New Caledonia: two new species of *Pancheria* (Cunoniaceae) from the Roche Ouaieme. . *Biodiversity and Conservation* **13**, 2253-73.

Bradshaw A. D. (1987) Restoration: an acid test for ecology. In: *Restoration ecology* (eds W. R. Jordan, M. Gilpin and J. D. Aber) pp. 23-9. Cambridge University Press, Cambridge.

Brook B. W. & Bowman D. (2006) Postcards from the past: charting the landscape-scale conversion of tropical Australian savanna to closed forest during the 20th century. *Landscape Ecology* **21**, 1253-66.

Brook B. W., Bradshaw C. J. A., Pin Koh L. & Sodhi N. S. (2006) Momentum Drives the Crash: Mass Extinction in the Tropics *Biotropica* **38**, 302-5.

Brooks M. L., D'Antonio C. M., Richardson D. M., Grace J. B., Keeley J. E., DiTomaso J. M., Hobbs R. J., Pellant M. & Pyke D. (2004) Effects of invasive alien plants on fire regimes. *Bioscience* **54**, 677-88.

Brooks T. M., Mittermeier R. A., Mittermeier C. G., da Fonseca G. A. B., Rylands A. B., Konstant W. R., Flick P., Pilgrim J., Oldfield S., Magin G. & Hilton-Taylor C. (2002) Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology* **16**, 909-23.

Brooks T. M., Pimm S. L. & Oyugi J. O. (1999) Time lag between deforestation and bird extinction in tropical forest fragments. *Conservation Biology* **13**, 1140-50.

Bucini G. & Hanan N. P. (2007) A continental-scale analysis of tree cover in African savannas. *Glob. Ecol. Biogeogr.* **16**, 593-605.

Cadenasso M. L., Pickett S. T. A., Weathers K. C. & Jones C. G. (2003) A framework for a theory of ecological boundaries. *Bioscience* **53**, 750-8.

Carpenter R. J., Read J. & Jaffre T. (2003) Reproductive traits of tropical rain-forest trees in New Caledonia. *Journal of Tropical Ecology* **19**, 351-65.

Cavelier J., Aide T. M., Santos C., Eusse A. M. & Dupuy J. M. (1998) The savannization of moist forests in the Sierra Nevada de Santa Marta, Colombia. *Journal of Biogeography* **25**, 901-12.

Chatain A., Read J. & Jaffre T. (2009) Does leaf-level nutrient-use efficiency explain Nothofagus-dominance of some tropical rain forests in New Caledonia? *Plant Ecology* **201**, 51-66.

Choesin D. & Boerner R. E. J. (2002) Vegetation boundary detection: A comparison of two approaches applied to field data. *Plant Ecology* **158**, 85-96.

Christensen J. H., Hewitson B., Busuioc A., Chen A., Gao X., Held I., Jones R., Kolli R. K., Known W.-T., Laprise R., Magaña Rueda V., Mearns L., Menéndez C. G., Räisänen J., Rinke A., Sarr A. & Whetton P. (2007) Regional climate projections. In: Climate Change 2007: The Physical Science Basis. In: *Contibution of Warking Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor and H. L. Miller), New York.

Clark J. S., Silman M., Kern R., Macklin E. & HilleRisLambers J. (1999) Seed dispersal near and far: Patterns across temperate and tropical forests. *Ecology* **80**, 1475-94.

Cochrane M. A. (2003) Fire science for rainforests. *Nature* **421**, 913-9.

Cochrane M. A., Alencar A., Schulze M. D., Souza C. M., Nepstad D. C., Lefebvre P. & Davidson E. A. (1999) Positive feedbacks in the fire dynamic of closed canopy tropical forests. *Science* **284**, 1832-5.

Cochrane M. A. & Laurance W. F. (2002) Fire as a large-scale edge effect in Amazonian forests. *Journal of Tropical Ecology* **18**, 311-25.

Cohen J. (1960) A coefficient of agreement for nominal scales. *Educational and Psychological Measurement* **20**, 37-46.

Cole R. J., Holl K. D. & Zahawi R. A. (2010) Seed rain under tree islands planted to restore degraded lands in a tropical agricultural landscape. *Ecol. Appl.* **20**, 1255-69.

Condit R., Ashton P. S., Baker P., Bunyavejchewin S., Gunatilleke S., Gunatilleke N., Hubbell S. P., Foster R. B., Itoh A., LaFrankie J. V., Lee H. S., Losos E., Manokaran N., Sukumar R. & Yamakura T. (2000) Spatial patterns in the distribution of tropical tree species. *Science* **288**, 1414-8.

Connell J. H. & Lowman M. D. (1989) Low-diversity tropical rain forests - Some possible mechanisms for their existence. *American Naturalist* **134**, 88-119.

Connell J. H. & Slatyer R. O. (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist* **111**, 1119-44.

Cornelius J. M. & Reynolds J. F. (1991) On determining the statistical significance of discontinuities with ordered ecological data. *Ecology* **72**, 2057-70.

Cottrell T. R. (2004) Seed rain traps for forest lands: Considerations for trap construction and study design. *Journal of Ecosystems and Management* **5**.

Couteron P., Seghieri J. & Chadoeuf J. (2003) A test for spatial relationships between neighbouring plants in plots of heterogeneous plant density. *Journal of Vegetation Science* **14**, 163-72.

Cramer J. M., Mesquita R. C. G. & Williamson G. B. (2007) Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees. *Biological Conservation* **137**, 415-23.

Crawford P. H. C. & Hoagland B. W. (2009) Can herbarium records be used to map alien species invasion and native species expansion over the past 100 years? *Journal of Biogeography* **36**, 651-61.

Cressie N. (1991) *Statistics for Spatial Data*. John Wiley and Sons, New York.

Cubina A. & Aide T. M. (2001) The effect of distance from forest edge on seed rain and soil seed bank in a tropical pasture. *Biotropica* **33**, 260-7.

Curt T., Borgniet L., Ibanez T., Hély C., Despinoy M. & Mangeas M. (in prep.) Spatial patterns of wildfires in New Caledonia : Implications for forest dynamics.

Dantonio C. M. & Vitousek P. M. (1992) Biological invasions by exotic grasses, the grass fire cycle, and global change. *Annual Review of Ecology and Systematics* **23**, 63-87.

Davis M. A., Wrage K. J., Reich P. B., Tjoelker M. G., Schaeffer T. & Muermann C. (1999) Survival, growth, and photosynthesis of tree seedlings competing with herbaceous vegetation along a water-light-nitrogen gradient. *Plant Ecology* **145**, 341-50.

De Garine I. & Lepoutre-Goffinet M. (2004) Les feux de brousses et de forêt en Province Sud: Aspects socioculturels. Direction Réserve Naturelle Province Sud, Nouméa.

De Garine-Wichatitsky M., Soubeyran Y., Maillard D. & Duncan P. (2005) The diets of introduced rusa deer (*Cervus timorensis russa*) in a native sclerophyll forest and a native rainforest of New Caledonia. *New Zealand Journal of Zoology* **32**, 117-26.

Delcroix T. & Lenormand O. (1997) ENSO signals in the vicinity of New Caledonia, South Western Pacific. *Oceanologica Acta* **20**, 481-91.

Denslow J. S. (2003) Weeds in paradise: Thoughts on the invasibility of tropical islands. *Annals of the Missouri Botanical Garden* **90**, 119-27.

Denslow J. S. (2007) Managing dominance of invasive plants in wildlands. *Curr. Sci.* **93**, 1579-86.

Denslow J. S., Uowolo A. L. & Hughes R. F. (2006) Limitations to seedling establishment in a mesic Hawaiian forest. *Oecologia* **148**, 118-28.

Dickinson M. B. & Johnson E. A. (2004) Temperature-dependent rate models of vascular cambium cell mortality. *Can. J. For. Res.-Rev. Can. Rech. For.* **34**, 546-59.

Didham R. K. & Lawton J. H. (1999) Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica* **31**, 17-30.

Diggle P. J. (2003) *Statistical Analysis of Point Patterns (2nd ed.)*. Oxford University Press, New York.

Dirzo R. & Raven P. H. (2003) Global state of biodiversity and loss. *Annual Review of Environment and Resources* **28**, 137-67.

Dobhal P. K., Kohli R. K. & Batish D. R. (2011) Impact of Lantana camara L. invasion on riparian vegetation of Nayar region in Garhwal Himalayas (Uttarakhand, India). *Journal of Ecology and the Natural Environment* **3**, 11-22.

Dray F. A., Bennett B. C. & Center T. D. (2006) Invasion history of *Melaleuca quinquenervia* (Cav.) S.T. Blake in Florida. *Castanea* **71**, 210-25.

Dray S. & Dufour A. B. (2004) The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software* **22**, 1-20.

Driscoll D. A., Lindenmayer D. B., Bennett A. F., Bode M., Bradstock R. A., Cary G. J., Clarke M. F., Dexter N., Fensham R., Friend G., Gill M., James S., Kay G., Keith D. A., MacGregor C., Russell-Smith J., Salt D., Watson J. E. M., Williams R. J. & York A. (2010) Fire management for biodiversity conservation: Key research questions and our capacity to answer them. *Biological Conservation* **143**, 1928-39.

Duggin J. A. & Gentle C. B. (1998) Experimental evidence on the importance of disturbance intensity for invasion of *Lantana camara* L. in dry rainforest-open forest ecotones in north-eastern NSW, Australia. *For. Ecol. Manage.* **109**, 279-92.

Elmqvist T., Wall M., Berggren A. L., Blix L., Fritioff A. & Rinman U. (2002) Tropical forest reorganization after cyclone and fire disturbance in Samoa: Remnant trees as biological legacies. *Conservation Ecology* **5**.

Enright N. J., Ogden J. & Rigg L. S. (1999) Dynamics of forests with Araucariaceae in the western Pacific. *Journal of Vegetation Science* **10**, 793-804.

Enright N. J., Rigg L. & Jaffre T. (2001) Environmental controls on species composition along a (maquis) shrubland to forest gradient on ultramafics at Mont Do, New Caledonia. *South African Journal of Science* **97**, 573-80.

Fagan W. F., Fortin M. J. & Soykan C. (2003) Integrating edge detection and dynamic modeling in quantitative analyses of ecological boundaries. *Bioscience* **53**, 730-8.

FAO. (2010) Global Forest Ressources Assessment 2010. In: *FAO Forestry paper*. Food and Agricultural Organisation of the United Nations, Rome, Italy.

Fink R. D., Lindell C. A., Morrison E. B., Zahawi R. A. & Holl K. D. (2009) Patch Size and Tree Species Influence the Number and Duration of Bird Visits in Forest Restoration Plots in Southern Costa Rica. *Restoration Ecology* **17**, 479-86.

Folke C., Carpenter S., Walker B., Scheffer M., Elmqvist T., Gunderson L. & Holling C. S. (2004) Regime shifts, resilience, and biodiversity in ecosystem management. *Annu. Rev. Ecol. Evol. Syst.* **35**, 557-81.

Fonsca C. R. & Joner F. (2007) Two-Sided Edge Effects Studies and the Restoration of Endegered Ecosystems *Restoration Ecology* **15**, 613-9.

Franklin J. & Rey S. J. (2007) Spatial patterns of tropical forest trees in Western Polynesia suggest recruitment limitations during secondary. *Journal of Tropical Ecology* **23**, 1-12.

Franklin J., Syphard A. D., Mladenoff D. J., He H. S., Simons D. K., Martin R. P., Deutschman D. & O'Leary J. F. (2001) Simulating the effects of different fire regimes on plant functional groups in Southern California. *Ecological Modelling* **142**, 261-83.

Fritsch E. (2011) Cartes des sols. In: *Atlas de la Nouvelle-Calédonie* (eds E. Habert, J. Bonvallot and J.-C. Gay). IRD, Nouméa.

Fuller D. O. & Murphy K. (2006) The ENSO-fire dynamic in insular Southeast Asia. *Climatic Change* **74**, 435-55.

Gailhbaud P. (2009) Modes de dispersion des diaspores sur le massif de l'Aoupinié, une forêt dense humide de Nouvelle-Calédonie. IRD, Nouméa.

Gambiza J., Campbell B. M., Moe S. R. & Frost P. G. H. (2005) Fire behaviour in a semi-arid *Baikiaea plurijuga* savanna woodland on Kalahari sands in western Zimbabwe. *South African Journal of Science* **101**, 239-44.

Garcillan P. P. & Ezcurra E. (2011) Sampling procedures and species estimation: testing the effectiveness of herbarium data against vegetation sampling in an oceanic island. *Journal of Vegetation Science* **22**, 273-80.

Gardner T. A. (2006) Tree-grass coexistence in the Brazilian cerrado: demographic consequences of environmental instability. *Journal of Biogeography* **33**, 448-63.

Gardner T. A., Barlow J., Chazdon R., Ewers R. M., Harvey C. A., Peres C. A. & Sodhi N. S. (2009) Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters* **12**, 561-82.

Gardner T. A., Barlow J., Parry L. W. & Peres C. A. (2007) Predicting the Uncertain Future of Tropical Forest Species in a Data Vacuum *Biotropica* **39**, 25-30.

Gargominy O., Bouchet P., Pascal M., Jaffré T. & Tourneur J. C. (1996) Consequences for biodiversity of plant and animal species introductions in New Caledonia. *Revue d'Ecologie-La Terre et la Vie* **51**, 375-402.

Gashaw M., Michelsen A., Friis I., Jensen M., Demissew S. & Woldu Z. (2002) Post-fire regeneration strategies and tree bark resistance to heating in frequently burning tropical savanna woodlands and grasslands in Ethiopia. *Nord. J. Bot.* **22**, 19-33.

Geiger E. L., Gotsch S. G., Damasco G., Haridasan M., Franco A. C. & Hoffmann W. A. (2011) Distinct roles of savanna and forest tree species in regeneration under fire suppression in a Brazilian savanna. *Journal of Vegetation Science* **22**, 312-21.

Gignoux J., Clobert J. & Menaut J. C. (1997) Alternative fire resistance strategies in savanna trees. *Oecologia* **110**, 576-83.

Gignoux J., Lahoreau G., Julliard R. & Barot S. (2009) Establishment and early persistence of tree seedlings in an annually burned savanna. *J. Ecol.* **97**, 484-95.

Gillespie T. W. & Jaffré T. (2003) Tropical dry forests in New Caledonia. *Biodiversity and Conservation* **12**, 1687-97.

Goldammer J. G. (1999) Ecology - Forests on fire. *Science* **284**, 1782-3.

Gonzales R. S., Ingle N. R., Lagunzad D. A. & Nakashizuka T. (2009) Seed Dispersal by Birds and Bats in Lowland Philippine Forest Successional Area. *Biotropica* **41**, 452-8.

Goreaud F. & Pelissier R. (1999) On explicit formulas of edge effect correction for Ripley's K-function. *Journal of Vegetation Science* **10**, 433-8.

Goreaud F. & Pelissier R. (2003) Avoiding misinterpretation of biotic interactions with the intertype K-12-function: population independence vs. random labelling hypotheses. *Journal of Vegetation Science* **14**, 681-92.

Govender N., Trollope W. S. W. & Van Wilgen B. W. (2006) The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. *Journal of Applied Ecology* **43**, 748-58.

Grandcolas P., Murienne J., Robillard T., Desutter-Grandcolas L., Jourdan H., Guilbert E. & Deharveng L. (2008) New Caledonia: A very old Darwinian island? *Philosophical Transactions of the Royal Society B-Biological Sciences* **363**, 3309-17.

Greene D. F. & Johnson E. A. (1989) A model of wind dispersal of winged or plumed seeds. *Ecology* **70**, 339-47.

Guevara S., Laborde J. & Sanchez-Rios G. (2004) Rain forest regeneration beneath the canopy of fig trees isolated in pastures of Los Tuxtlas, Mexico. *Biotropica* **36**, 99-108.

Guevara S., Purata S. E. & Vandermaarel E. (1986) The role of remnant forest trees in tropical secondary succession. *Vegetatio* **66**, 77-84.

Guisan A., Edwards T. C. & Hastie T. (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling* **157**, 89-100.

Guisan A. & Thuiller W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters* **8**, 993-1009.

Guisan A. & Zimmermann N. E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling* **135**, 147-86.

Gunderson L. H. (2000) Ecological resilience - in theory and application. *Annual Review of Ecology and Systematics* **31**, 425-39.

Haase P. (1995) Spatial pattern-analysis in ecology based on Ripley K-function - Introduction and methods of edge correction. *Journal of Vegetation Science* **6**, 575-82.

Halpern C. B., Antos J. A., Rice J. M., Haugo R. D. & Lang N. L. (2010) Tree invasion of montane meadow complex: temporal trends, spatial patterns, and biotic interactions. *Journal of Vegetation Science* **21**, 717-32.

Hart T. B., Hart J. A. & Murphy P. G. (1989) Monodominant and species-rich forests of the humid tropics - Causes for their co-occurence. *American Naturalist* **133**, 613-33.

Hastie T. & Tibshirani R. (1986) Generalized Additive Models. *Statistical Science* **1**, 297-318.

Hély C. & Alleaume S. (2006) Fire regimes in dryland landscapes. In: *Dryland Ecohydrology* (eds C. M. D'Odorico and A. Porporato) pp. 283-301. Springer, Netherlands.

Hely C., Dowty P. R., Alleaume S., Caylor K. K., Korontzi S., Swap R. J., Shugart H. H. & Justice C. O. (2003) Regional fuel load for two climatically contrasting years in southern Africa. *J. Geophys. Res.-Atmos.* **108**, 17.

Hély C., Tinquaut F., Ibanez T., Curt T., Géraux H. & Finney M. (in prep.) Is the New-Caledonian tropical forest burning? A model-data comparison.

Hennenberg K. J., Fischer F., Kouadio K., Goetze D., Orthmann B., Linsenmair K. E., Jeltsch F. & Porembski S. (2006) Phytornass and fire occurrence along forest-savanna transects in the Comoe National Park, Ivory Coast. *Journal of Tropical Ecology* **22**, 303-11.

Hennenberg K. J., Goetze D., Kouame L., Othmann B. & Porembski S. (2005a) Border and ecotone detection by vegetation composition along forest-savanna transcts in Ivory Coast. *Journal of Vegetation Science* **16**, 301-10.

Hennenberg K. J., Goetze D., Minden V., Traoré D. & Porembski S. (2005b) Size-class distribution of *Anogeissus leiocarpus* (Combretaceae) along forest-savanna ecotones in northern Ivory Coast. *Journal of Tropical Ecology* **21**, 273-81.

Hennenberg K. J., Goetze D., Szarzynski J., Orthmann B., Reineking B., Steinke I. & Porembski S. (2008) Detection of seasonal variability in microclimatic borders and ecotones between forest and savanna. *Basic and Applied Ecology* **9**, 275-85.

Hequet V., Le Corre M., Rigault F. & Blanfort V. (2009) Les espèces exotiques végétales envahissantes de Nouvelle-Calédonie. IRD, Nouméa.

Herrera J. M. & Garcia D. (2010) Effects of Forest Fragmentation on Seed Dispersal and Seedling Establishment in Ornithochorous Trees. *Conservation Biology* **24**, 1089-98.

Higgins S. I., Bond W. J. & Trollope W. S. W. (2000) Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *J. Ecol.* **88**, 213-29.

Hirota M., Holmgren M., Van Nes E. H. & Scheffer M. (2011) Global Resilience of Tropical Forest and Savanna to Critical Transitions. *Science* **334**, 232-5.

Hoffa E. A., Ward D. E., Hao W. M., Susott R. A. & Wakimoto R. H. (1999) Seasonality of carbon emissions from biomass burning in a Zambian savanna. *J. Geophys. Res.-Atmos.* **104**, 13841-53.

Hoffmann W. A. (1996) The effects of fire and Cover on seedling establishement in a neotropical savanna. *J. Ecol.* **84**, 383-93.

Hoffmann W. A. (2000) Post-establishement seedling success in the Brazilian Cerrado: A comparaison of savanna and forest species. *Biotropica* **32**, 62-9.

Hoffmann W. A., Adasme R., Haridasan M., de Carvalho M. T., Geiger E. L., Pereira M. A. B., Gotsch S. G. & Franco A. C. (2009) Tree topkill, not mortality, governs the dynamics of savanna-forest boundaries under frequent fire in central Brazil. *Ecology* **90**, 1326-37.

Hoffmann W. A. & Haridasan M. (2008) The invasive grass, Melinis minutiflora, inhibits tree regeneration in a Neotropical savanna. *Austral Ecology* **33**, 29-36.

Hoffmann W. A., Lucatelli V., Silva F. J., Azeuedo I. N. C., Marinho M. D., Albuquerque A. M. S., Lopes A. D. & Moreira S. P. (2004) Impact of the invasive alien grass *Melinis minutiflora* at the savanna-forest ecotone in the Brazilian Cerrado. *Divers Distributions* **10**, 99-103.

Hoffmann W. A., Orthen B. & Do Nascimento P. K. V. (2003) Comparative fire ecology of tropical savanna and forest trees. *Functional Ecology* **17**, 720-6.

Hoffmann W. A. & Solbrig O. T. (2003) The role of topkill in the differential response of savanna woody species to fire. *For. Ecol. Manage.* **180**, 273-86.

Holl K. D. (1998) Do bird perching structures elevate seed rain and seedling establishment in abandoned tropical pasture? *Restoration Ecology* **6**, 253-61.

Holl K. D. (1999) Factors limiting tropical rain forest regeneration in abandoned pasture: Seed rain, seed germination, microclimate, and soil. *Biotropica* **31**, 229-42.

Holl K. D., Loik M. E., Lin E. H. V. & Samuels I. A. (2000) Tropical montane forest restoration in Costa Rica: Overcoming barriers to dispersal and establishment. *Restoration Ecology* **8**, 339-49.

Hooper E., Legendre P. & Condit R. (2005) Barriers to forest regeneration of deforested and abandoned land in Panama. *Journal of Applied Ecology* **42**, 1165-74.

Hope G. & Pask J. (1998) Tropical vegetational change in the late Pleistocene of New Caledonia. *Palaeogeography Palaeoclimatology Palaeoecology* **142**, 1-21.

Hopkins H. C. F. (2006) Nomenclature and typification in Geissois (Cunoniaceae) in the South-West Pacific. *243-254* **28**, 311-27.

Hopkins H. C. F., Fogliani B. & Pillon Y. (2007) Four new species in the endemic genus *Codia* (*Cunoniaceae*) from New Caledonia. *Kew Bulletin* **62**, 259-74.

Horowitz L. S. (2001) Perceptions of nature and responses to environmental degradation in New Caledonia. *Ethnology* **40**, 237-50.

Hovestadt T., Yao P. & Linsenmair K. E. (1999) Seed dispersal mechanisms and the vegetation of forest islands in a West African forest-savanna mosaic (Comoe National Park, Ivory Coast). *Plant Ecology* **144**, 1-25.

Hufkens K., Scheunders P. & Ceulemans R. (2009) Ecotones in vegetation ecology: methodologies and definitions revisited. *Ecol. Res.* **24**, 977-86.

Ibanez T., Curt T. & Hély C. (submitted-a) Estimated fire injuries highlight low fire tolerance of New Caledonian savannas trees
. *Journal of Vegetation Science*.

Ibanez T., Géraux H., Meandu-Poveu D. & Hély C. (in prep.-a) Low seed-rain but enhanced by perch effect in a New Caledonian savanna. *Restoration Ecology*.

Ibanez T., Hély C., Curt T. & Gaucherel C. (in prep.-b) Sharp transition of microclimatic conditions at the rainforest-savanna boundary in New Caledonia: Insights for rainforest edge vulnerability to fire.

Ibanez T., L. B., Mangeas M., Gaucherel C., Géraux H. & Hély C. (submitted-b) Rainforest and Savanna Landscape Dynamics in New Caledonia: Towards a Mosaic of Stable Rainforest and Savanna states? *Austal Ecology*.

Ibanez T., Munzinger J., Gaucherel C., Curt T. & Hély C. (in prep.-c) Key species and ecological structure detecting savanna-forest transiton zone dynamics in New Caledonia.

Ibanez T., Munzinger J., Géraux H., Gaucherel C. & Hély C. (submitted-c) Mono-dominated and co-dominated early secondary succession patterns in New Caledonia. *Biotropica*.

Illian J., Penttinen A., Stoyan H. & Stoyan D. (2008) *Statistical Analysis and Modelling of Spatial Point Patterns*. Wiley, Chichester.

Jackson J. F., Adams D. C. & Jackson U. B. (1999) Allometry of constitutive defense: A model and a comparative test with tree bark and fire regime. *American Naturalist* **153**, 614-32.

Jaffré T. (1993) Relation between ecological diversity and floristic diversity in New Caledonia. *Biodiversity Letters* **1**, 82 - 91.

Jaffré T., Bouchet P. & Veillon J. M. (1998) Threatened plants of New Caledonia: Is the system of protected areas adequate? *Biodiversity and Conservation* **7**, 109-35.

Jaffré T., Morat P., Veillon J. M., Rigault F. & Dagostini G. (2001) *Composition et caractérisation de la flore indigène de Nouvelle-Calédonie / Composition and characterisation of the native flora of New Caledonia*. IRD, Nouméa.

Jaffre T., Munzinger J. & Lowry P. P. (2010) Threats to the conifer species found on New Caledonia's ultramafic massifs and proposals for urgently needed measures to improve their protection. *Biodiversity and Conservation* **19**, 1485-502.

Jaffré T., Rigault F., Dagostini G., Tinel-Fambart J., Wulff A. & Munzinger J. (2009) Input of the different vegetation units to the richness and endemicity of the New Caledonian flora. In: *Pacific Science Intercongress*, Tahiti, France.

Jaffré T., Rigault F. & Munzinger J. (2008) Identification and characterization of floristic groups in dry forests relicts of a West Coast region of New Caledonia. *Pacific Conservation Biology* **14**, 128-45.

Jaffré T. & Veillon J. M. (1994) Les principales formations végétales autochtones en Nouvelle Calédonie : caractéristiques, vulnérabilité, mesures de sauvegardes. In: *Sciences de la vie, biodiversité* (ed R. d. synthèses). ORSTOM (IRD), Nouméa.

Jaffré T. & Veillon J. M. (1995) Structural and floristic characteristics of a rain forest on schist in New Caledonia : a comparaison with an ultramafic rain forest. *Bull. Mus. natl. Hist. nat., B, Adansonia, 4è sér.* **17**, 201-26.

Jaffré T., Veillon J. M. & Pintaud J. C. (1997a) Comparaison de la diversité floristique des forêt denses humides sur roches ultramafiques et substrats différents en Nouvelle-Calédonie. In: *Ecologie des milieux sur roches ultramafiques et des sols métallifères* (eds T. Jaffre, R. D. Reeves and T. Becquer) pp. 163-70. Orstom, Nouméa.

Jaffré T., Veillon J. M., Rigault F. & Dagostini G. (1997b) Impact des feux de brousse sur la flore et les groupement végétaux de Nouvelle Calédonie. In: *Rapport Cordet*. ORSTOM, Nouméa.

Jansen R. K., Cai Z., Raubeson L. A., Daniell H., Depamphilis C. W., Leebens-Mack J., Muller K. F., Guisinger-Bellian M., Haberle R. C., Hansen A. K., Chumley T. W., Lee S. B., Peery R., McNeal J. R., Kuehl J. V. & Boore J. L. (2007) Analysis of 81 genes from 64 plastid genomes resolves relationships in angiosperms and identifies genome-scale evolutionary patterns. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 19369-74.

Kalema J. (2008) The use of herbarium plant databases in identifying areas of biodiversity concentration: the case of family Acanthaceae in Uganda. *African Journal of Ecology* **46**, 125-6.

Kauffman J. B., Cummings D. L. & Ward D. E. (1994) Relationships of fire, biomass and nutrient dynamics along a vegetation gradient in the Brazilian Cerrado. *J. Ecol.* **82**, 519-31.

Keeley J. E. (2009) Fire intensity, fire severity and burn severity: a brief review and suggested usage. *Int. J. Wildland Fire* **18**, 116-26.

Kellman M. & Meave J. (1997) Fire in the tropical gallery forests of Belize. *Journal of Biogeography* **24**, 23-34.

Kikvidze Z. & Ohsawa M. (2002) Measuring the number of co-dominants in ecological communities. *Ecol. Res.* **17**, 519-25.

King J., Moutsinga J.-B. & Doufoulon G. (1997) Conversion of anthropogenic savanna to production forest through fire-protection of the forest-savanna edge in Gabon, Central Africa *For. Ecol. Manage.* **94**, 233-47.

Lamb D., Erskine P. D. & Parrotta J. A. (2005) Restoration of degraded tropical forest landscapes. *Science* **310**, 1628-32.

Laurance W. F. (2007) Have we overstated the tropical biodiversity crisis? *Trends Ecol. Evol.* **22**, 65-70.

Laurance W. F. & Curran T. J. (2008) Impacts of wind disturbance on fragmented tropical forests: A review and synthesis. *Austral Ecology* **33**, 399-408.

Law R., Illian J., Burslem D., Gratzer G., Gunatilleke C. V. S. & Gunatilleke I. (2009) Ecological information from spatial patterns of plants: insights from point process theory. *J. Ecol.* **97**, 616-28.

Lawes M. J., Adie H., Russell-Smith J., Murphy B. & Midgley J. (2011) How do small savanna trees avoid stem mortality by fire? The roles of stem diameter, height and bark thickness. *Ecosphere* **2**.

Le Page Y., Pereira J. M. C., Trigo R., da Camara C., Oom D. & Mota B. (2008) Global fire activity patterns (1996-2006) and climatic influence: an analysis using the World Fire Atlas. *Atmospheric Chemistry and Physics* **8**, 1911-24.

Lehmann C. E. R., Prior L. D., Williams R. J. & Bowman D. (2008) Spatio-temporal trends in tree cover of a tropical mesic savanna are driven by landscape disturbance. *Journal of Applied Ecology* **45**, 1304-11.

Levey D. J., Bolker B. M., Tewksbury J. J., Sargent S. & Haddad N. M. (2005) Effects of landscape corridors on seed dispersal by birds. *Science* **309**, 146-8.

Lewis S. L. (2006) Tropical forests and the changing earth system. *Philosophical Transactions of the Royal Society B-Biological Sciences* **361**, 195-210.

Li W. H., Dickinson R. E., Fu R., Niu G. Y., Yang Z. L. & Canadell J. G. (2007) Future precipitation changes and their implications for tropical peatlands. *Geophys. Res. Lett.* **34**, 6.

Liebsch D., Marques M. C. M. & Goldenbeg R. (2008) How long does the Atlantic Rain Forest take to recover after a disturbance? Changes in species composition and ecological features during secondary succession. *Biological Conservation* **141**, 1717-25.

Liedloff A. C. & Cook G. D. (2007) Modelling the effects of rainfall variability and fire on tree populations in an Australian tropical savanna with the FLAMES simulation model. *Ecological Modelling* **201**, 269-82.

Linares-Palomino R. & Kessler M. (2009) The role of dispersal ability, climate and spatial separation in shaping biogeographical patterns of phylogenetically distant plant groups in seasonally dry Andean forests of Bolivia. *Journal of Biogeography* **36**, 280-90.

Loiselle B. A., Jorgensen P. M., Consiglio T., Jimenez I., Blake J. G., Lohmann L. G. & Montiel O. M. (2008) Predicting species distributions from herbarium collections: does climate bias in collection sampling influence model outcomes? *Journal of Biogeography* **35**, 105-16.

Lopez-Zamora I., Comerford N. B. & Muchovej R. M. (2004) Root development and competitive ability of the invasive species *Melaleuca quinquenervia* (Cav.) ST Blake in the South Florida flatwoods. *Plant Soil* **263**, 239-47.

Love A., Babu S. & Babu C. R. (2009) Management of Lantana, an invasive alien weed, in forest ecosystems of India. *Curr. Sci.* **97**, 1421-9.

Lowry II P. P. (1998) Diversity, endemism, and extinction in the flora of New Caldeonia: A review. In: *Proc. Intl. Symposium on Rare, Threatened and Endangered Floras of Asia and the Pacific* (eds C.-I. Peng and P. P. Lowry, II) pp. 181-206. Academia Sinica, Taipei, Taiwan.

Ludwig J. A. & Cornelius J. M. (1987) Locating discontinuities along ecological gradients. *Ecology* **68**, 448-50.

Mack M. C. & D'Antonio C. M. (1998) Impacts of biological invasions on disturbance regimes. *Trends Ecol. Evol.* **13**, 195-8.

Maharjan S. K., Poorter L., Holmgren M., Bongers F., Wieringa J. J. & Hawthorne W. D. (2011) Plant Functional Traits and the Distribution of West African Rain Forest Trees along the Rainfall Gradient. *Biotropica* **43**, 552-61.

Matlack G. R. (1993) Microenvironment variation within and among forest edge sites in the eastern United States. *Biological Conservation* **66**, 185-94.

Mayer A. L. & Khalyani A. H. (2011) Grass Tumps Trees with Fire. *Science* **334**, 188-9.

McClanahan T. R. & Wolfe R. W. (1987) Dispersal of orhithochorous seeds from forest edges in central Florida. *Vegetatio* **71**, 107-12.

McCook L. J. (1994) Understanding ecological community succession - causal-models and theories, a review. *Vegetatio* **110**, 115-47.

McCoy S., Jaffré T., Rigault F. & Ash J. E. (1999) Fire and succession in the ultramafic maquis of New Caledonia. *Journal of Biogeography* **26**, 579-94.

McCullagh P. & Nelder J. A. (1989) *Generalized Linear Models*. Chapman and Hall, London.

McDonnell M. J. & Stiles E. W. (1983) The structural complexity of old field vegetation and the recruitment of bird-dispersed plant-species. *Oecologia* **56**, 109-16.

McPherson G. (1991) Euphorbiaceae - Phyllanthoideae. *Antidesma, Bischofia, Breynia, Cleistanthus, Drypetes, Glochidion*. In: *Flore de la Nouvelle-Calédonie et Dépendances* (eds P. Morat and H. S. MacKee) pp. 3-30. Muséum National d'Histoire Naturelle, Paris.

Meave J., Kellman M., Macdougall A. & Rosales J. (1991) Riparian habitats as tropical forest refugia. *Glob. Ecol. Biogeogr. Lett.* **1**, 69-76.

Medellin R. A. & Gaona O. (1999) Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico. *Biotropica* **31**, 478-85.

METEO-France. (2007) *Atlas climatique de la Nouvelle Calédonie* METEO-France en Nouvelle Calédonie, Nouméa.

Michaletz S. T. & Johnson E. A. (2006) A heat transfer model of crown scorch in forest fires. *Can. J. For. Res.-Rev. Can. Rech. For.* **36**, 2839-51.

Michaletz S. T. & Johnson E. A. (2007) How forest fires kill trees: A review of the fundamental biophysical processes. *Scand. J. Forest Res.* **22**, 500-15.

Michaletz S. T. & Johnson E. A. (2008) A biophysical process model of tree mortality in surface fires. *Can. J. For. Res.-Rev. Can. Rech. For.* **38**, 2013-29.

Midgley J. J., Lawes M. J. & Chamaille-Jammes S. (2010) Savanna woody plant dynamics: the role of fire and herbivory, separately and synergistically. *Aust. J. Bot.* **58**, 1-11.

Millenium Ecosystem Assessment. (2005) Ecosystems and Human Well-being: Synthesis. (ed I. Press), Washington, DC.

Mistry J. & Berardi A. (2005) Assessing fire potential in a Brazilian savanna nature reserve. *Biotropica* **37**, 439-51.

Mittermeier R. A., Robles Gil P., Hoffmann M., Pilgrim J., Brooks T., Mittermeier C. G., Lamoureux J. & da Fonseca G. A. B. (2004) *Hotspots Revisted*. Chicago University Press, Chicago.

Moran P. A. P. (1950) Notes on continuous stochastic phenomena. *Biometrika* **37**, 17-23.

Morat P., Jaffre T., Tronchet F., Munzinger J., Pillon Y., Veillon J. M. & Chalopin M. (in prep.) The taxonomic reference base "Florical" and characteristics of the native vascular flora of New Caledonia. *243-254* **Submitted**.

Morat P., Jaffre T., Tronchet F., Munzinger J., Pillon Y., Veillon J. M. & Chalopin M. (Submitted) The taxonomic reference base "Florical" and characteristics of the native vascular flora of New Caledonia. *243-254* **Submitted**.

Morrison E. B. & Lindell C. A. (2011) Active or Passive Forest Restoration? Assessing Restoration Alternatives with Avian Foraging Behavior. *Restoration Ecology* **19**, 170-7.

Müller S. C., Overbeck G. E., Pfadenhauer J. & Pillar V. D. (2007) Plant functional types of woody species related to fire disturbance in forest-grassland ecotones. *Plant Ecology* **189**, 1-14.

Muller-Landau H. C., Wright S. J., Calderon O., Condit R. & Hubbell S. P. (2008) Interspecific variation in primary seed dispersal in a tropical forest. *J. Ecol.* **96**, 653-67.

Murcia C. (1995) Edge effects in fragmented forests - implications for consevation. *Trends Ecol. Evol.* **10**, 58-62.

Murienne J. (2009) Testing biodiversity hypothesis in New Caledonia using phylogenetics. *Journal of Biogeography* **36**, 1433-4.

Murienne J., Grandcolas P., Piulachs M. D., Bellés X., D'Haese C., Legendre F., Pellens R. & Guilbert E. (2005) Evolution on a shaky piece of Gondwana: is local endemism rescent in New Caledonia? *Cladistics* **21**, 2-7.

Murphy B. P. & Russell-Smith J. (2010) Fire severity in a northern Australian savanna landscape: the importance of time since previous fire. *Int. J. Wildland Fire* **19**, 46-51.

Myers N. (1988) Threatened biotas: "hot spots" in tropical forests. *Environmentalist* **8**, 187-208.

Myers N. (2003) Biodiversity hotspots revisited. *Bioscience* **53**, 916-7.

Myers N., Mittermeier R. A., Mittermeier C. G., da Fonseca G. A. B. & Kent J. (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**, 853-8.

Myers R. L. (1983) Site Susceptibility to invasion by the exotic tree *Melaleuca quinquenervia* in southern Florida. *Journal of Applied Ecology* **20**, 645-58.

Nathan R. & Muller-Landau H. C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. Evol.* **15**, 278-85.

Nathan R., Safriel U. N. & Noy-Meir I. (2001) Field validation and sensitivity analysis of a mechanistic model for tree seed dispersal by wind. *Ecology* **82**, 374-88.

Nepstad D., Carvalho G., Barros A. C., Alencar A., Capobianco J. P., Bishop J., Moutinho P., Lefebvre P., Silva U. L. & Prins E. (2001) Road paving, fire regime feedbacks, and the future of Amazon forests. *For. Ecol. Manage.* **154**, 395-407.

Nepstad D. C., Verissimo A., Alencar A., Nobre C., Lima E., Lefebvre P., Schlesinger P., Potter C., Moutinho P., Mendoza E., Cochrane M. & Brooks V. (1999) Large-scale impoverishment of Amazonian forests by logging and fire. *Nature* **398**, 505-8.

Nicet J. B. & Delcroix T. (2000) ENSO-related precipitation changes in New Caledonia, southwestern tropical Pacific: 1969-98. *Monthly Weather Review* **128**, 3001-6.

Ohtsuka T. (1999) Early stages of secondary succession on abandoned cropland in north-east Borneo Island. *Ecol. Res.* **14**, 281-90.

Olson D. M. & Dinerstein E. (2002) The Global 200: Priority ecoregions for global conservation. *Annals of the Missouri Botanical Garden* **89**, 199-224.

Ortega-Pieck A., Lopez-Barrera F., Ramirez-Marcial N. & Garcia-Franco J. G. (2011) Early seedling establishment of two tropical montane cloud forest tree species: The role of native and exotic grasses. *For. Ecol. Manage.* **261**, 1336-43.

Paine C. E. T., Stahl C., Courtois E. A., Patino S., Sarmiento C. & Baraloto C. (2010) Functional explanations for variation in bark thickness in tropical rain forest trees. *Functional Ecology* **24**, 1202-10.

Parr C. L. & Andersen A. N. (2006) Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. *Conservation Biology* **20**, 1610-9.

Pascal M., Richer de Forges B. R., Le Guyader H. & Simberloff D. (2008) Mining and other threats to the New Caledonia biodiversity hotspot. *Conservation Biology* **22**, 498-9.

Pauchard A., Garcia R. A., Peña E., Gonzales C., Cavieres L. A. & Bustamante R. O. (2008) Positive feedbacks between plant invasion and fire regimes: Teline

monspessulana (L.) K. Koch (Fabaceae) in central Chile. *Biological Invasions* **10**, 547-53.

Pelissier R. (1998) Tree spatial patterns in three contrasting plots of a southern Indian tropical moist evergreen forest. *Journal of Tropical Ecology* **14**, 1-16.

Pelissier R. & Goreaud F. (2001) A practical approach to the study of spatial structure in simple cases of heterogeneous vegetation. *Journal of Vegetation Science* **12**, 99-108.

Pelissier R. & Goreaud F. (2009) ads: Spatial point patterns analysis.

Pena-Claros M. (2003) Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon. *Biotropica* **35**, 450-61.

Perry G. L. W. & Enright N. J. (2002a) Humans, fire and landscape pattern: understanding a maquis-forest complex, Mont Do, New Caledonia, using a spatial 'state-and-transition' model. *Journal of Biogeography* **29**, 1143-58.

Perry G. L. W. & Enright N. J. (2002b) Spatial modelling of landscape composition and pattern in a maquis-forest complex, Mont Do, New Caledonia. *Ecological Modelling* **152**, 279-302.

Perry G. L. W., Enright N. J. & Jaffre T. (2001) Spatial modelling of landscape-scale vegetation dynamics, Mont Do, New Caledonia. *South African Journal of Science* **97**, 501-9.

Perry G. L. W., Miller B. P. & Enright N. J. (2006) A comparison of methods for the statistical analysis of spatial point patterns in plant ecology. *Plant Ecology* **187**, 59-82.

Perry J. N., Liebhold A. M., Rosenberg M. S., Dungan J., Miriti M., Jakomulska A. & Citron-Pousty S. (2002) Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. *Ecography* **25**, 578-600.

Peterson D. L. & Ryan K. C. (1986) Modeling postfire conifer mortality for long-range planning. *Environmental Management* **10**, 797-808.

Pillon Y., Munzinger J., Amir H., Hopkins H. C. F. & Chase M. W. (2009) Reticulate evolution on a mosaic of soils: diversification of the New Caledonian endemic genus *Codia* (Cunoniaceae). *Molecular Ecology* **18**, 2263-75.

Pillon Y. & Nooteboom H. P. (2009) A new species of Symplocos (Symplocaceae) from Mont Panie (New Caledonia). *243-254* **31**, 191-6.

Pinard M. A. & Huffman J. (1997) Fire resistance and bark properties of trees in a seasonally dry forest in eastern Bolivia. *Journal of Tropical Ecology* **13**, 727-40.

Pizo M. A. (2004) Frugivory and habitat use by fruit-eating birds in a fragmented landscape of southeast Brazil. *Ornitol. Neotrop.* **15**, 117-26.

Pratt P. D., Quevedo V., Bernier L., Sustache J. & Center T. D. (2005) Invasions of Puerto Rican wetlands by the Australian tree *Melaleuca quinquenervia*. *Caribbean Journal of Science* **41**, 42-54.

Prevedello J. A. & Vieira M. V. (2010) Does the type of matrix matter? A quantitative review of the evidence. *Biodiversity and Conservation* **19**, 1205-23.

R Development Core Team. (2009) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Raedig C., Dormann C. F., Hildebrandt A. & Lautenbach S. (2010) Reassessing Neotropical angiosperm distribution patterns based on monographic data: a geometric interpolation approach. *Biodiversity and Conservation* **19**, 1523-46.

Raghubanshi A. S. & Tripathi A. (2009) Effect of disturbance, habitat fragmentation and alien invasive plants on floral diversity in dry tropical forests of Vindhyan highland: a review. *Tropical Ecology* **50**, 57-69.

Ratnam J., Bond W. J., Fensham R. J., Hoffmann W. A., Archibald S., Lehmann C. E. R., Anderson M. T., Higgins S. I. & Sankaran M. (2011) When is a 'forest' a savanna, and why does it matter? *Glob. Ecol. Biogeogr.* **20**, 653-60.

Raup D. M. (1986) Biological Extinction in Earth History. *Science* **231**, 1528-33.

Ray D., Nepstad D. & Brando P. (2010) Predicting moisture dynamics of fine understory fuels in a moist tropical rainforest system: results of a pilot study undertaken to identify proxy variables useful for rating fire danger. *New Phytologist* **187**, 720-32.

Ray D., Nepstad D. & Moutinho P. (2005) Micrometeorological and canopy controls of fire susceptibility in a forested Amazon landscape. *Ecol. Appl.* **15**, 1664-78.

Rayamajhi M. B., Van T. K., Center T. D., Goolsby J. A., Pratt P. D. & Racelis A. (2002) Biological attributes of the canopy-held *Melaleuca* seeds in Australia and Florida, US. *J. Aquat. Plant Manage.* **40**, 87-91.

Read J., Hallam P. & Cherrier J. F. (1995) The anomaly of monodominant tropical rain-forests - some preliminary-observations in the *Nothophagus*-dominated rain-forests of New-Caledonia. *Journal of Tropical Ecology* **11**, 359-89.

Read J., Jaffre T., Ferris J. M., McCoy S. & Hope G. S. (2006) Does soil determine the boundaries of monodominant rain forest with adjacent mixed rain forest and maquis on ultramafic soils in New Caledonia? *Journal of Biogeography* **33**, 1055-65.

Reis A., Bechara F. C. & Tres D. R. (2010) Nucleation in tropical ecological restoration. *Scientia Agricola* **67**, 244-50.

Rigg L. S., Enright N. J., Perry G. L. W. & Miller B. P. (2002) The role of cloud combing and shading by isolated trees in the succession from maquis to rain forest in New Caledonia. *Biotropica* **34**, 199-210.

Ripley B. D. (1976) The second-order analysis of stationary point processes. *Journal of applied Probability* **13**, 255-66.

Roberts C. M., McClean C. J., Veron J. E. N., Hawkins J. P., Allen G. R., McAllister D. E., Mittermeier C. G., Schueler F. W., Spalding M., Wells F., Vynne C. & Werner T. B. (2002) Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* **295**, 1280-4.

Ropelewski C. F. & Halpert M. S. (1987) Global and regional scale precipitation patterns associated with the El-Niño Southern Oscillation. *Monthly Weather Review* **115**, 1606-26.

Rossatto D. R., Hoffmann W. A. & Franco A. C. (2009) Differences in growth patterns between co-occurring forest and savanna trees affect the forest-savanna boundary. *Functional Ecology* **23**, 689-98.

Russell-Smith J., Stanton P. J., Edwards A. C. & Whitehead P. J. (2004a) Rain forest invasion of eucalypt-dominated woodland savanna, Iron Range, north-eastern Australia: II. Rates of landscape change. *Journal of Biogeography* **31**, 1305-16.

Russell-Smith J., Stanton P. J., Whitehead P. J. & Edwards A. C. (2004b) Rain forest invasion of eucalypt-dominated woodland savanna, Iron Range, north-eastern Australia: I. Successional processes. *Journal of Biogeography* **31**, 1305-16.

Ryan K. C. & Reinhardt E. D. (1988) Predicting postfire mortality of seven western conifers. *Can. J. For. Res.* **18**, 1291-7.

Sankaran M., Hanan N. P., Scholes R. J., Ratnam J., Augustine D. J., Cade B. S., Gignoux J., Higgins S. I., Le Roux X., Ludwig F., Ardo J., Banyikwa F., Bronn A., Bucini G., Caylor K. K., Coughenour M. B., Diouf A., Ekaya W., Feral C. J., February E. C., Frost P. G. H., Hiernaux P., Hrabar H., Metzger K. L., Prins H. H. T., Ringrose S., Sea W., Tews J., Worden J. & Zambatis N. (2005) Determinants of woody cover in African savannas. *Nature* **438**, 846-9.

Sankaran M., Ratnam J. & Hanan N. P. (2004) Tree-grass coexistence in savannas revisited - insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters* **7**, 480-90.

Sarlin P. (1954) Bois et forêts de la Nouvelle-Calédonie. (ed C. t. f. tropical). Centre technique forestier tropical, Nogent-sur-Marne.

Savadogo P., Zida D., Sawadogo L., Tiveau D., Tigabu M. & Oden P. C. (2007) Fuel and fire characteristics in savanna-woodland of West Africa in relation to grazing and dominant grass type. *Int. J. Wildland Fire* **16**, 531-9.

Scheffer M., Carpenter S., Foley J. A., Folke C. & Walker B. (2001) Catastrophic shits in ecosystems. *Nature* **413**, 591-6.

Scheffer M. & Carpenter S. R. (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol. Evol.* **18**, 648-56.

Schlawin J. & Zahawi R. A. (2008) 'Nucleating' succession in recovering neotropical wet forests: The legacy of remnant trees. *Journal of Vegetation Science* **19**, 485-U7.

Scholes R. J. & Archer S. R. (1997) Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* **28**, 517-44.

Schroder A., Persson L. & De Roos A. M. (2005) Direct experimental evidence for alternative stable states: a review. *Oikos* **110**, 3-19.

Scutz A. E. N. & Bond W. J. (2009) Junggling carbon allocation patterns of a dominant tree in a fire prone savanna. *Oecologia* **160**, 235-46.

Sebert H. (1874) *Notice sur les bois de la Nouvelle-Calédonie, suivi de considération générales sur les propriétés mécaniques des bois et sur les procédés employés pour les mesurer*. Arthus Bertrand, Paris.

Secretariat of the Convention on Biological Diversity. (2001) Impacts of human-caused fires on biodiversity and ecosystems functionning, and their causes in tropical, temperate and boreal forest biomes. (ed S. o. t. C. o. B. Diversity), Montreal.

Seidler T. G. & Plotkin J. B. (2006) Seed dispersal and spatial pattern in tropical trees. *PLoS. Biol.* **4**, 2132-7.

Sekercioglu C. H. (2006) Increasing awareness of avian ecological function. *Trends Ecol. Evol.* **21**, 464-71.

Serbesoff-King K. (2003) *Melaleuca* in Florida: A literature review on the taxonomy, distribution, biology, ecology, economic importance and control measures. *J. Aquat. Plant Manage.* **41**, 98-112.

SGT. (2008) Classification de l'occupation du sol de la Nouvelle-Calédonie par approche objet réalisée par le Service de la Géomatique et de la télédétecion du Gouvernement de Nouvelle-Calédonie. Nouméa.

Shea R. W., Shea B. W., Kauffman J. B., Ward D. E., Haskins C. I. & Scholes M. C. (1996) Fuel biomass and combustion factors associated with fires in savanna ecosystems of South Africa and Zambia. *J. Geophys. Res.-Atmos.* **101**, 23551-68.

Sherley G. (2000) Invasive species in the Pacific: A technical review and draft regional strategy. (ed S. P. R. E. P. (SPREP)), Apia, Samoa.

Shiels A. B. & Walker L. R. (2003) Bird perches increase forest seeds on Puerto Rican landslides. *Restoration Ecology* **11**, 457-65.

Sidiyasa K. (1998) Taxonomy, Phylogeny, and Wood anatomy of *Alstonia* (Apocynaceae). *Blumea* **Supplement 11**, 1-230.

Siegert F., Ruecker G., Hinrichs A. & Hoffmann A. A. (2001) Increased damage from fires in logged forests during droughts caused by El Nino. *Nature* **414**, 437-40.

Silva L. C. R., Sternberg L., Haridasan M., Hoffmann W. A., Miralles-Wilhelm F. & Franco A. C. (2008) Expansion of gallery forests into central Brazilian savannas. *Glob. Change Biol.* **14**, 2108-18.

Sloan S. (2007) Fewer People May Not Mean More Forest For Latin American Forest Frontiers. *Biotropica* **39**, 443-6.

Slocum M. G. (2001) How tree species differ as recruitment foci in a tropical pasture. *Ecology* **82**, 2547-59.

Slocum M. G. & Horvitz C. C. (2000) Seed arrival under different genera of trees in a neotropical pasture. *Plant Ecology* **149**, 51-62.

Smith A. M. S., Wooster M. J., Drake N. A., Dipotso F. M., Falkowski M. J. & Hudak A. T. (2005) Testing the potential of multi-spectral remote sensing for retrospectively estimating fire severity in African Savannahs. *Remote Sens. Environ.* **97**, 92-115.

Soltis D. E., Soltis P. S., Chase M. W., Mort M. E., Albach D. C., Zanis M., Savolainen V., Hahn W. H., Hoot S. B., Fay M. F., Axtell M., Swensen S. M., Prince L. M., Kress W. J., Nixon K. C. & Farris J. S. (2000) Angiosperm phylogeny inferred from 18S rDNA, rbcL, and atpB sequences. *Botanical Journal of the Linnean Society* **133**, 381-461.

Staver A. C., Archibald S. & Levin S. (2011a) Tree cover in sub-Saharan Africa: Rainfall and fire constrain forest and savanna as alternative stable states. *Ecology* **92**, 1063-72.

Staver A. C., Archibald S. & Levin S. A. (2011b) The Global Extent and Determinants of Savanna and Forest as Alternative Biome States *Science* **334**, 230-2.

Steffen W., Sanderson A., Tyson P. D., Jäger J., Matson P. A., Moore III B., Oldfield F., Richardson K., Schellnhuber H. J., Turner II B. L. & Wasson R. J. (2004) *Global Change and the Earth System: A Planet Under Presure*, New York.

Stephens S. L. & Libby W. J. (2006) Anthropogenic fire and bark thickness in coastal and island pine populations from Alta and Baja California. *Journal of Biogeography* **33**, 648-52.

Stevenson J. (2004) A late-Holocene record of human impact from the southwest coast of New Caledonia. *Holocene* **14**, 888-98.

Stevenson J., Dodson J. R. & Prosser I. P. (2001) A late Quaternary record of environmental change and human impact from New Caledonia. *Palaeogeography Palaeoclimatology Palaeoecology* **168**, 97-123.

Stevenson J. & Hope G. (2005) A comparison of late Quaternary forest changes in New Caledonia and northeastern Australia. *Quaternary Research* **64**, 372-83.

Stocks B. J., vanWilgen B. W., Trollope W. S. W., McRae D. J., Mason J. A., Weirich F. & Potgieter A. L. F. (1996) Fuels and fire behavior dynamics on large-scale savanna fires in Kruger National Park, South Africa. *J. Geophys. Res.-Atmos.* **101**, 23541-50.

Stork N. E. (2010) Re-assessing current extinction rates. *Biodiversity and Conservation* **19**, 357-71.

Stott P. (2000) Combustion in tropical biomass fires: a critical review. *Progress in Physical Geography* **24**, 355-77.

Stoyan D. & Penttinen A. (2000) Recent applications of point process methods in forestry statistics. *Statistical Science* **15**, 61-78.

Strayer D. L., Power M. E., Fagan W. F., Pickett S. T. A. & Belnap J. (2003) A classification of ecological boundaries. *Bioscience* **53**, 723-9.

Svenning J. C., Kinner D. A., Stallard R. F., Engelbrecht B. M. J. & Wright S. J. (2004) Ecological determinism in plant community structure across a tropical forest landscape. *Ecology* **85**, 2526-38.

Swaine M. D., Hawthorne W. D. & Orgle T. K. (1992) The effects of fire exclusion on savanna vegetation at Kpong, Ghana. *Biotropica* **24**, 166-72.

Tackenberg O., Poschlod P. & Bonn S. (2003) Assessment of wind dispersal potential in plant species. *Ecol. Monogr.* **73**, 191-205.

Thompson I., Mackey B., McNulty S. & Mosseler A. (2009) Forest Resilience, Biodiversity, and Climate Change. A synthesis of the biodiversity / resilience / stability relationship in forest ecosystems. In: *Technical Series* p. 67. Secretariat of the Convention on Biological Diversity, Montreal.

Tirel C. & Veillon J.-M. (2002) Pittosporaceae. In: *Flore de la Nouvelle-Calédonie et Dépendances* (ed P. Morat) pp. 1-178. Muséum National d'Histoire Naturelle, Paris.

Toh I., Gillespie M. & Lamb D. (1999) The role of isolated trees in facilitating tree seedling recruitment at a degraded sub-tropical rainforest site. *Restoration Ecology* **7**, 288-97.

Torti S. D., Coley P. D. & Kursar T. A. (2001) Causes and consequences of monodominance in tropical lowland forests. *American Naturalist* **157**, 141-53.

Turner C. E., Center T. D., Burrows D. W. & Buckingham G. R. (1998) Ecology and management of *Melaleuca quinquenervia*, an invader of wetlands in Florida, U.S.A. *Wetlands Ecology and Management* **5**, 165-78.

Udo N. (2011) Feu, ressources naturelles et territoires: Perceptions, usages et mode de gestion. In: *Rapport de stage de Master 2*. Université Montpellier II.

van der Werf G. R., Randerson J. T., Giglio L., Gobron N. & Dolman A. J. (2008a) Climate controls on the variability of fires in the tropics and subtropics. *Glob. Biogeochem. Cycle* **22**, 13.

van der Werf G. R., Randerson J. T., Giglio L., Gobron N. & Dolman A. J. (2008b) Climate controls on the variability of fires in the tropics and subtropics. *Glob. Biogeochem. Cycle* **22**.

van Langevelde F., van de Vijver C., Kumar L., van de Koppel J., de Ridder N., van Andel J., Skidmore A. K., Hearne J. W., Stroosnijder L., Bond W. J., Prins H. H. T. & Rietkerk M. (2003) Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* **84**, 337-50.

van Mantgem P. & Schwartz M. (2003) Bark heat resistance of small trees in Californian mixed conifer forests: testing some model assumptions. *For. Ecol. Manage.* **178**, 341-52.

Van Nieuwstadt M. G. L. & Sheil D. (2005) Drought, fire and tree survival in a Borneo rain forest, East Kalimantan, Indonesia. *J. Ecol.* **93**, 191-201.

Van T. K., Rayamajhi M. B. & Center T. D. (2005) Seed longevity of *Melaleuca quinquenervia*: A burial experiment in South Florida. *J. Aquat. Plant Manage.* **43**, 39-42.

Van Wagner C. E. (1973) Height of crown scorch in forest fires. *Can. J. For. Res.* **3**, 373-8.

van Welzen P. C. (1989) *Guioa Cav. (Sapindaceae): taxonomy, phylogeny and historical biogeography*. Rijksherbarium/Hortus botanicus, Leiden.

Vanwilgen B. W. & Wills A. J. (1988) Fire behavior prediction in savanna vegetation. *South Afr. J. Wildl. Res.* **18**, 41-6.

Veldman J. W. & Putz F. E. (2011) Grass-dominated vegetation, not species-diverse natural savanna, replaces degraded tropical forests on the southern edge of the Amazon Basin. *Biological Conservation* **144**, 1419-29.

Vesk P. A. (2006) Plant size and resprouting ability: trading tolerance and avoidance of damage? *J. Ecol.* **94**, 1027-34.

Virot R. (1956) *La végétation canaque*. Mémoire du muséum national d'histoire naturelle.

Walker S., Wilson J. B., Steel J. B., Rapson G. L., Smith B., King W. M. & Cottam Y. H. (2003) Properties of ecotones: Evidence from five ecotones objectively determined from a coastal vegetation gradient. *Journal of Vegetation Science* **14**, 579-90.

Warman L. & Moles A. T. (2009) Alternative stable states in Australia's Wet Tropics: a theoretical framework for the field data and a field-case for the theory. *Landscape Ecology* **24**, 1-13.

Watt M. S., Kriticos D. J. & Manning L. K. (2009) The current and future potential distribution of *Melaleuca quinquenervia*. *Weed Research* **49**, 381-90.

Whelan C. J., Wenny D. G. & Marquis R. J. (2008) Ecosystem services provided by birds. In: *Year in Ecology and Conservation Biology 2008* (eds R. S. Ostfeld and W. H. Schlesinger) pp. 25-60.

Whelan R. J. (1995) *The Ecology of Fire*. Cambridge University Press, Cambridge.

Wiegand T., Martinez I. & Huth A. (2009) Recruitment in Tropical Tree Species: Revealing Complex Spatial Patterns. *American Naturalist* **174**, E106-E40.

Wiegand T. & Moloney K. A. (2004) Rings, circles, and null-models for point pattern analysis in ecology. *Oikos* **104**, 209-29.

Williams P. R., Congdon R. A., Grice A. C. & Clarke P. J. (2005) Effect of season of burning and removal of herbaceous cover on seedling emergence in a eucalypt savanna of north-eastern Australia. *Austral Ecology* **30**, 491-6.

Williams R. J., Cook G. D., Gill A. M. & Moore P. H. R. (1999) Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. *Australian Journal of Ecology* **24**, 50-9.

Williams R. J., Gill A. M. & Moore P. H. R. (1998) Seasonal changes in fire behaviour in a tropical Savanna in Northern Australia. *Int. J. Wildland Fire* **8**, 227-39.

Williams R. J., Gill A. M. & Moore P. H. R. (2003) Fire behaviour. In: *Fire in Tropical Savannas: The Kapalaga Experiment* (eds A. N. Andersen, G. D. Cook and R. J. Williams) pp. 33-46. Springer, New York.

Wirrmann D., Semah A. M. & Chacornac-Rault M. (2006) Late Holocene paleoenvironment in northern New Caledonia, southwestern Pacific, from a multiproxy analysis of lake sediments. *Quaternary Research* **66**, 213-+.

Wood S. N. (2001) mgcv : GAMs and Generalized Ridge Regression for R. *R News* **1**, 20-5.

Wright S. J. & Muller-Landau H. C. (2006a) The future of tropical forest species. *Biotropica* **38**, 287-301.

Wright S. J. & Muller-Landau H. C. (2006b) The Uncertain Futur of Tropical Forest Species. *Biotropica* **38**, 443-5.

Zimmerman J. K., Pascarella J. B. & Aide T. M. (2000) Barriers to forest regeneration in an abandoned pasture in Puerto Rico. *Restoration Ecology* **8**, 350-60.